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1981

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OVERVIEW

SYSTEMATICS AND DEVELOPMENT OF EARLY LIFE HISTORY STAGES OF MARINE FISHES: ACHIEVEMENTS DURING THE PAST CENTURY, PRESENT STATUS AND SUGGESTIONS FOR THE FUTURE

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The overview of the field of Systematics and Development that we prepared for the meetings was a more extensive version than the present account. In this condensed version we will still attempt to deal with the basic questions asked in the initial version: How did our discipline develop? Where are we now? What about the future?

HISTORICAL BACKGROUND

In 1865 G. O. Sars, the eminent Norwegian planktonologist, observed that the cod had pelagic eggs and larvae. However, it was not until 1879, just a century ago, that Sars published his impressive, milestone epoch-making investigation on the cod fisheries of the Lofoten Islands reporting on the complete life history of the cod, from pelagic eggs and pelagic larvae to juvenile and adult stages.

Sars' work on cod stimulated interest in pelagic fish eggs and larvae, in general, and it was soon found that most of the species of commercial interest had floating eggs and larvae. The initial impetus was in rearing fish eggs and larvae to determine characters that would permit their identification in plankton collections. During the last two decades of the 19th Century prodigious research activity centered in England, Italy and Germany. Notable among the early enthusiastic workers in Great Britain were J. T. Cunningham, E. W. L. Holt, W. C. McIntosh, E. E. Prince, and A. T. Masterman; who worked mainly between 1885 and 1900. Simultaneously in Italy, a triad of scientists were conducting pioneering investigations; C. Emery, L. Facciola, and F. Raffaele, who published in the years between 1878 to 1900. Other early workers of consequence include Alexander Agassiz from the USA and E. Ehrenbaum and Fr. Heinicke in Germany.

The rationale for conducting ichthyoplankton surveys was well-stated by Johan Hjort (Murray and Hjort, 1912) in "The Depth of the Oceans."

> "This power of distinguishing the different species in early stages has been of great advantage to oceanography. By securing the eggs and larvae floating in the surface waters, we can decide what species spawn in a definite area. We capture in our silk nets a profusion of different eggs and larvae, and can with certain limitations separate them as belonging to various species, just as we assort the catches of adult fishes from a haul with the trawl. The spawning area of a species can thus be determined by merely taking numerous tow-nettings and ascertaining the presence or absence of the eggs belonging to the species in question."

In 1900, the Norwegians activated a research vessel, the "Michael Sars," for open sea work; and in 1901, Hjort conducted an ichthyoplankton survey off northern Norway where he succeeded in finding areas of abundant cod spawning. At the time, there was no fishery for cod in the area, but his discovery stimulated a fishery that soon took some millions of cod. Hjort described the research:

> "Stimulated by this experience I advised the International Council for the Study (sic) of the Sea to effect a systematic survey of the spawning areas of the cod family. My proposals were adopted and an

> enormous amount of material relating to the natural history of the cod family was accumulated, thanks to the exertions of those on board the Danish, Belgian, English, Scottish, Dutch, Norwegian, Swedish and German investigation steamers.
>
> "The Danish steamer, "Thor," under the leadership of Schmidt, investigated certain parts of the Atlantic and the waters round Iceland. The Norwegian steamer, "Michael Sars," examined the Norwegian Sea and the northern portion of the North Sea, while the steamers of the other countries worked mainly in the North Sea."

This joint investigation conducted in 1901 was one of ICES earliest undertakings in obtaining a wealth of information about the spawning areas and biology of the various gadoids. More importantly, they stimulated research on ichthyoplankton in a number of countries.

Collections obtained during this cooperative research venture from the Danish research steamer, "Thor," in 1903 and 1904 were to be worked up into classic papers by C. G. J. Petersen and J. Schmidt. Petersen devoted much of his research efforts to obtaining complete life history series of flatfishes, while Schmidt's main early thrust was with gadoid life history series. Between 1905 and 1907, Schmidt published six contributions dealing with gadoid larvae. Altogether, Schmidt described life history series for 17 kinds of gadoids. His contributions are landmarks, that set high standards of quality for establishing and presenting life history series that have challenged all subsequent workers.

Schmidt is perhaps best known for his work locating the breeding ground of the European eel (*Anguilla vulgaris*), by studying the distribution of its leptocephali in the North Atlantic. The eel research furnished impetus for the Dana Round the World Expedition of 1928–30.

Because space limitations do not permit a more extended discussion of the historical background, we have prepared a summary table listing some of the more important contributions to deal with early life history series of marine teleost fishes (Table 1).

PRESENT STATUS

We next wish to address the question — where are we now? Since the end of World War II, we have witnessed major advances in our knowledge of fish eggs and larvae on a worldwide scale and major advances in the quality of the papers being published. Our discipline, on the whole, is in a healthy state.

There are two basic ways to establish life history series of eggs and larvae. One rears eggs and larvae to determine their characters; or one uses ichthyoplankton collections to construct series working backwards from juveniles to larvae and eggs. The rearing approach using eggs and milt of known adults can be carried out most successfully with inshore fishes, or with commercial species that are fished throughout the year. Few of the offshore epipelagic species and none of the mesopelagic or bathypelagic species have been reared from artificially fertilized eggs. Although it is preferable to begin with eggs of known parents, much recent work utilizes live eggs obtained from plankton hauls for rearing. With improvement in rearing techniques, this method has

Table 1. Some of the more important contributions dealing with early life history series of marine teleost fishes (see also Table 2).

		No.		Source		Stages			
Scientist	Date	contributions	Group dealt with	Field coll.	Rearing	Egg	Larvae	Juv Ad.	Area
Petersen, C. G. J.	1904–09	3	Flatfishes	X	—	—	all	some	E. North Atlantic
Schmidt, J.	1905–07	6	Gadoid	X	—	—	all	some	E. North Atlantic
Schmidt, J.	1908–32	ca. 44	Eels, Mar. teleosts	X	—	—	all	some	N. Atl. — Worldwide
Ehrenbaum, E.	1905–09	book	Mar. teleosts	X	X	some	all	some	E. North Atlantic
Sanzo, L.	1905–40	ca. 65	Mar. teleosts	X	X	some	all	some	Mediterranean
Kyle, H. M.	1913	1	Flatfishes	X	—	—	all	some	Medit. — adj. N. Atl.
Fage, L.	1918	1	Shorefishes	X	—	—	most	some	Medit. — adj. N. Atl
Tåning, A. V.	1918	1	Myctophids	X	—	—	all	all	Medit. — adj. N. Atl.
Jespersen and Tåning	1919–26	2	Sternoptychids	X	—	some	all	some	Medit. and E. North Atl.
Delsman, H. C.	1921–38	24	Mar. teleosts	X	X	some	most	some	Indo Pacific
Hildebrand and Cable	1930–38	3	Shore-Bay fishes	X	X	most	all	most	W. North Atlantic
D'Ancona et al.	1931–56	4 parts	Mar. teleosts	X	X	many	most	some	Mediterranean
Uchida et al.	1958	1	Mar. teleosts	X	X	some	all	some	Off Japan
Mito, S.	1960–63	12	Pelagic fish eggs	X	X	all	all	—	Off Japan
Castle, P. H. J.	1959 to date	many	Eels	X	X	some	all	some	Off N. Z. — also worldwide
Dekhnik, T. V.	1973	1	Ichthyoplankton	X	X	most	most	—	Black Sea

proven very useful for constructing life history series. The advantage of rearing is that complete larval series in prime condition can often be obtained and identified as post-larvae or juveniles.

Two technical advances have greatly aided studies of early life history series of fishes. The more important for larval studies are the techniques for clearing and staining specimens in order to follow sequence of ossification as well as to make precise counts of meristic characters. The other involves use of x-rays for making radiographs for determining internal osteological features.

Internal characters that can be studied on cleared and stained specimens are becoming increasingly important in identification of larvae. Among the internal characters are those associated with the vertebral column, with supporting bones for fins, with head bones, etc. For example, the character of pterygiophores and their arrangement in relation to vertebral spines can be quite useful, or the number and arrangement of pre-dorsal bones or the supporting bones for the caudal fin, etc. (Potthoff, 1974; Ahlstrom et al., 1976). One of our contributions introduced the dynamic approach for larval descriptions (Ahlstrom and Ball, 1954). In this approach the sequence of changes occurring during the larval period are treated character by character.

During the present decade we have given seven concentrated courses on the identification of fish eggs and larvae and one of the by-products of this has been the challenge to assemble characters of both adults and larvae that will permit the investigator to assign specimens to order or suborder as the first step in identification. The basic characters that the larval fish taxonomist has to work with are fourfold: (1) body shape (morphometrics); (2) pigment patterns; (3) countable structures (meristics); and (4) characters that are strictly larval. We give meristic characters more emphasis than morphometric because complete counts of fin rays, vertebrae, branchiostegal rays, etc. are usually obtained during the larval period, whereas body shape, while sometimes helpful, can change markedly between the larval and later life stages. Pigment patterns are of most use in distinguishing among species within a genus or between genera within a family, but seldom at higher taxonomic levels. Characters that are exclusively larval can be very useful in identification to the family level and sometimes to genus or species. We have found that the only convenient way of assembling such a mass of data is in tables. A set of such tables was included in our contribution given at the 2nd Ichthyological Congress in Paris (Ahlstrom and Moser, 1976).

For what portion of marine fish do we have early life history series? In "Fishes of the World" Nelson (1976), 450 familes of fishes are recognized. Of these, about 300 families fall into our area of interest; i. e., marine fishes that have pelagic eggs and/or pelagic larvae that can be captured by plankton net.

In our concentrated courses of identification of fish eggs and larvae, we study over 200 life history series representing 100 fish families. The course covers eggs and/or larvae of about 1/3 of the families that comprise the marine fish fauna. Eggs and/or larvae are known for about 110 additional marine families, hence early life history stages are known for over 2/3 of the families. What about the families whose eggs and larvae are not known yet? These are mostly small families, or those with bathypelagic distributions.

POTENTIAL FUTURE DIRECTIONS

The literature provides the basis for identifying the majority of marine fish larvae to family, genus or species, even in previously unsurveyed waters. Nearshore species and speciose tropical faunas have been particularly difficult to identify and are a challenge for the future. Our ability to solve difficult identification problems can be enhanced in several ways — by improving the quality of the specimens, by critically evaluating the characters we now use, and by discovering new characters.

Proper preservation of ichthyoplankton has always been a problem and each of us has had the experience of trying to identify poorly preserved material. The problem is particularly apparent when working with early larval stages and with material collected in the tropics. Research is needed on shipboard handling and preservation techniques, and advances in these areas could improve the effectiveness of ichthyoplankton surveys. Research is also needed in the area of long-term storage of specimens, particularly to solve such problems as fading of pigment characters, leaching of calcium from bony structures, and deterioration of tissues.

Identification of ichthyoplankton could be enhanced by a critical evaluation of the characters that are presently in use. Character variability has rarely been treated adequately and is an area of potentially valuable research. First on the list of variation studies is melanistic pigmentation. We need to know more about variation in number and morphological appearance of melanophores. What is the variability within broods, populations, and species? The shape or form of certain melanophores is often used in descriptions and identifications. How does this vary among individuals, particularly in relation to time of day or depth of capture? Melanophore pattern and number is such an important character for ichthyoplankton identification, especially for embryonic and early larval stages, that we could benefit greatly from research into the nature of these characters. Similarly, more information is needed on variation in morphometric and meristic characters. What are the limits of variability of body measurements and proportions that we use to distinguish species and higher taxa? Variation in countable characters is sometimes well known for juveniles and adults, but is seldom treated in larval descriptions. Do larvae show a greater variability in meristic characters than adults?

The search for new characters is never ending and certainly many remain to be discovered for fish eggs and larvae. Internal characters have received more attention in recent years. Developmental osteology has become a field in its own right and increased knowledge there has helped greatly in solving difficult taxonomic problems. With the advent of cartilage stains, the potential for solving difficult diagnostic problems is expanded further. Internal soft structures, especially those of the digestive tract, offer similar potential for solving special problem identifications or even in routine identification.

The elucidation of fine surface structures by scanning electromicroscopy (SEM) has potential for solving special taxonomic problems. For example, Sumida et al. (1979) used scanning electromicrographs to distinguish differences between chorion structure of *Pleuronichthys* and *Synodus* eggs. These differences were not apparent at lower magnification under a stereomicroscope but, once demonstrated by use of the SEM, they could be seen by careful study under a stereomicroscope. Similar application of the SEM may be useful in determining differences in spination, scale structure, or skin surface pattern of closely related larval species.

As mentioned in the historical review, rearing of fish larvae had a central role in the beginning of ichthyoplankton research. In the past, technical requirements for rearing marine fishes have limited its use in identification of eggs and larvae. Recent advances in the culture of food organisms (e.g., dinoflagellates, rotifers and copepods) and the increased availability of rearing facilities permit more widespread use of this valuable approach. For some difficult taxonomic problems involving large numbers of closely related species, such as in the scorpaenid genus *Sebastes* which contains about 100 species, rearing provides the only hope for differentiating the large residue of unidentified species. In addition to providing larval series preserved in prime condition and at desired ontogenetic stages, rearing offers the opportunity to study the effect of diet and environmental conditions, such as light and temperature, on character variability.

The use of developmental stages to gain insights into systematic relationships and to make phylogenetic inferences has a long history in vertebrate biology. This approach is especially useful when the larval stages have undergone an adaptive radiation that is separate from the juveniles and adults, as in anurans and teleosts. It is clear that for some groups of marine fishes the larval and adult worlds are distinctly separate evolutionary realms and, as a result, a rich array of larval characters may be added to the list of adult characters for systematic analysis.

Bertelsen's (1951) monograph on deep-sea anglerfishes was the first to utilize the characters of larvae in a comprehensive revision of a major group of marine fishes. By using a combination of ontogenetic and adult characters he was able to solve the major problems surrounding sexual dimorphism, species diagnosis, and higher relationships within this confusing group. Other workers have recognized the value of larval characters in elucidating systematic relationships and have used these characters to varying extents in taxonomic papers (Table 2). This approach has been particularly useful in treating myctophiform families, but recent studies on scorpaeniform, pleuronectiform, and perciform families suggest that larval characters may have wide application among higher teleosts.

At present, many ichthyologists recognize the potential for using larval characters in systematic revisions and it has become standard practice to attempt to locate and borrow larval material for such studies. With the growth of ichthyoplankton studies and the increased availability of larval material, we look forward to more frequent inclusion of early life history stages in systematic revisions of fishes.

The use of computers in phylogenetic studies of teleosts is widespread, however, larval characters have not yet been included in these analyses. In groups with highly evolved larval stages it would be interesting to compare the results of numerical analyses run on larvae and adults. The addition of larval characters to those of the adults in cladistic analysis is promising. Another potential use of computers is as a substitute for taxonomic keys. Dichotomous keys are difficult or impossible to construct for larvae since the essence of ontogenetic characters is change. A broad array of characters covering meristics, morphometry, pigmentation, distribution, season of occurrence, and relative abundance could be assembled and programmed to sort an unknown specimen down to the most likely species or group of species.

To conclude, our discipline has a distinguished past, and has become increasingly sophisticated in recent years, but many challenging problems remain for future research.

Table 2. Some contributions in which ontogenetic characters are used to clarify systematic relationships.

Scientists	Date	No. contri-butions	Group dealt with	Stages			Larval characters showing relationships			
				Egg	Larvae	Juv. Ad.	Among species	Among genera	Among subfam. or families	Among orders
Ege, Vilh.	1931–57	3	Paralepididae	—	+	±	X	X		
Bertelsen, E.	1951	1	Ceratioidei	—	+	+	X	X	X	
Bertelsen and Marshall	1956	1	Miripinnati	—	+	±	X	X	X	
Pertseva-Ostroumova, T. A.	1961	1	Pleuronectidae	+	+	±	X	X		
Pertseva-Ostroumova, T. A.	1965	1	Myctophidae	—	+	—	X	X		
Berry, F.	1964	1	Mar. teleosts	—	+	—				X
Moser and Ahlstrom	1970–74	3	Myctophidae	—	+	±	X	X	X	
Gutherz, E. J.	1970	1	Bothidae	—	+	—		X		
Mead, G. W.	1972	1	Bramidae	—	+	+	X	X		
Ahlstrom, E. H.	1974	1	Sternoptychidae	—	+	±	X	X		
Johnson, R. K.	1974	1	Scopelarchidae	—	+	+	X	X		
Okiyama, M.	1974	1	Myctophiformes	—	+	—		X	X	
Potthoff, T.	1974	1	Scombridae	—	+	+	X			
Richards and Potthoff	1974	1	Scombridae	—	+	±	X			
Aboussouan, A.	1975	1	Carangidae	—	+	—	X	X		
Ahlstrom, Butler and Sumida	1976	1	Stromateoidei	±	+	±	X	X	X	
Ahlstrom, Moser and O'Toole	1976	1	Myctophidae	—	+	+		X		
Bertelsen, Krefft and Marshall	1976	1	Notosudidae	—	+	±	X	X		
Ahlstrom and Moser	1976	1	Mar. teleosts	+	+	+				X
Moser, Ahlstrom and Sandknop	1977	1	Scorpaenidae	—	+	±	X	X	X	
Futch, C. R.	1977	1	Bothidae	—	+	—		X	X	
Powles and Stender	1978	1	Sciaenidae	—	+	±		X		
Richardson, S.	Symp. contri.	1	Cottidae	—	+	+		X		
Okiyama and Ueyanagi	1978	1	Scombridae	—	+	—		X	X	
Kendall, A.	1979	1	Serranidae	—	+	+		X	X	

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THE RELATION BETWEEN THE DISTRIBUTION OF ZOOPLANKTON PREDATORS AND ANCHOVY LARVAE

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The plankton collections analyzed for this study correspond to the monthly California Cooperative Oceanic Fisheries Investigation (CalCOFI) cruises of 1954, 1956, 1958. These years were selected because they were respectively "slightly colder", "colder", and "warmer" than the long-term average for the California Current. The total plankton was analyzed for species of Chaetognatha, Siphonophorae, Chondrophorae, Medusae and Ctenophora. Predation by these zooplankters has been observed frequently by planktologists, who find larvae in various stages of digestion in the guts of these predators, which are more effective on actively swimming large fish larvae than on relatively passive yolk-sac larvae.

Data on the distribution and abundance of larvae of the northern anchovy (*Engraulis mordax*) were compared with concentrations of predator species. Anchovy eggs were not included in the analysis due to the feeding characteristics of the predatory zooplankters, which respond primarily to movement or chemical agents, stimuli that are not provided by eggs.

While analyzing collections for the five groups of invertebrate predators, information was also taken on other zooplankton groups which occurred abundantly in the collections; Copepods, Euphausiids, Decapod larvae, Pteropods, Heteropods, Polychaetes, Salps, Doliolids and Pyrosomes.

METHODS

For each collection, individuals of the five predator groups were identified to species and the number of individuals were counted for the total sample. Counts from each sample were standardized to the number per 1000 m^3 of water strained. Other observations taken simultaneously included stage of sexual maturity, phase of life cycle, and occurrence of food in the stomach. Partially digested organisms in stomachs which evidenced feeding previous to collection, were identified.

Altogether more than 2000 plankton samples were analyzed. The CalCOFI collections were usually obtained with a net, 1 m in diameter at its mouth, hauled obliquely from 140 m depth, or less in shallow waters, to the surface. The CalCOFI collections were grouped into three categories with respect to abundance of anchovy larvae per standard haul; anchovy rich (more than 241 larvae), anchovy poor (1–240 larvae), and anchovy lacking (zero anchovy larvae per standard haul).

KINDS AND ABUNDANCE OF PREDATORY SPECIES

Altogether 22 species of Chaetognatha, 48 Siphonophorae, 34 Medusae, 3 Ctenophora, and 1 Chondrophorae were recorded. Variations in the composition of species of all groups were observed in the 3 years. Tropical species were taken mainly in 1958, the warmer than average year. The highest variability occurred in the Medusae, which usually show erratic distribution in time and space. Agalmid Siphonophorae are among the most successful predators, as they move swiftly through the waters acting as living nets capturing other plankters. *Stephanomia bijuga*, the most abundant agalmid in the CalCOFI collections, could be one of the primary predators on fish larvae. Ctenophores, except Beroë, were infrequently taken. These organisms are often destroyed by preservation, hence the numbers recorded are underestimations of their true abundance in the collections. Ctenophores float at or near the surface, and their predatory activity would be limited to this zone.

Yearly abundance of Chaetognatha,

Siphonophorae and Medusae were compared for the three categories of anchovy larvae abundance [high, low, and zero (Fig. 1)]. Chaetognatha were abundant in all three types of hauls. It should be noted that the two most abundant chaetognaths, *S. euneritica* and *S. bierii* are not considered important as predators on fish larvae, whereas, as discussed below, the three species of chaetognaths considered to be prime predators occurred less frequently and usually in less abundance in anchovy rich hauls. In 1956 samples there was little difference in abundance in all three groups of predators in the three categories of anchovy hauls. In 1954 and 1958 Siphonophorae were less abundant in anchovy rich hauls. A striking inverse relation between abundance of Medusae and abundance of anchovy larvae is evidenced in the 1954 and 1958 collections.

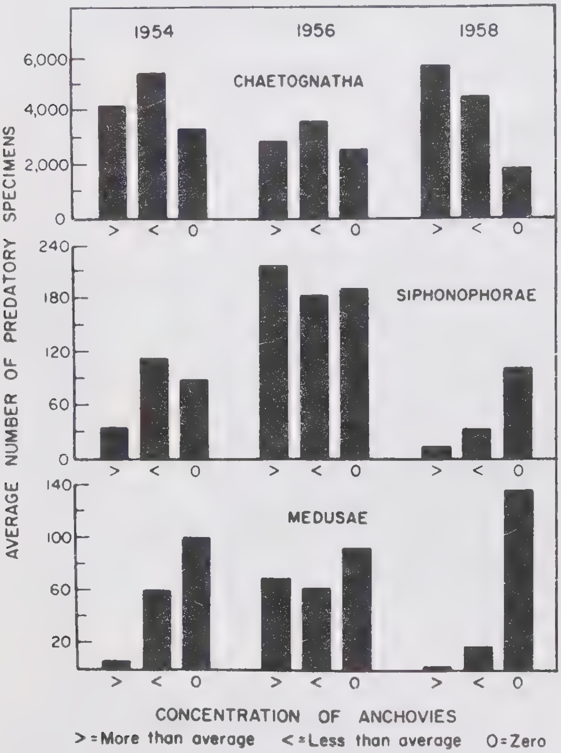

Figure 1. Yearly abundance of predators (Chaetognatha, Siphonophorae, Medusae) and concentration of anchovy larvae (high = more than 241 larvae per standard haul; low = 1–240 anchovy larvae per standard haul; zero = absence of anchovy larvae).

The predatory potential of an individual is roughly proportional to its size, and the predatory potential of the species is related to both size and abundance.

Based on these criteria, a selection was made from among the three principal groups of species considered to be primary candidates as effective predators on fish larvae. Those selected for separate study were the chaetognaths *Sagitta enflata*, *S. hexaptera*, *S. scrippsae*; the Siphonophorae *Chelophyes appendiculata*, *Diphyes dispar*, *Stephanomia bijuga*; and the Medusae *Liriope tetraphylla*, *Rhopalonema velatum*, *Aglaura hemistoma*. In each species recurrence and abundance were analyzed for anchovy rich and anchovy lacking hauls for each of the 3 years. Altogether these nine species, during 3 years result in 27 comparisons. In 24 of these the predator species occurred in greatest or major abundance in hauls lacking anchovy larvae, and in all 27 the frequency of occurrence of predator species was higher in hauls lacking anchovy larvae than in those with large aggregations of larvae (Table 1).

RELATION OF UPWELLING AND ANCHOVY LARVAE

Sagitta decipiens (mesopelagic chaetognath) can be used as an indicator of upwelling (Alvariño, 1965; Nair, 1977; Nair and Rao, 1973). Upwelling based on *S. decipiens* was most intense in 1956, intermediate in 1958, and low in 1954, which agrees with Bakun (1973) and Wyllie (1966). *S. decipiens* occurred in 2.8% of

Table 1. Most abundant large species of predators, and highest and zero concentration of anchovy larvae during 1954, 1956, 1958.

Abundance of anchovy larvae:	1954				1956				1958			
	High		Zero		High		Zero		High		Zero	
Species abundance: Species	% occur.	Aver. occup.	% occur.	Aver. occup.	% occur.	Aver. occup.	% occur.	Aver. occup.	% occur.	Aver. occup.	% occur.	Aver. occup.
Sagitta enflata	56	491.3	73	1 093.7	43	191.8	47	121.6	74	271.6	82	308.4
S. hexaptera	22	5.5	55	16.1	27	1.8	53	62.0	26	15.5	52	42.2
S. scrippsae	33	48.1	52	19.2	20	3.2	33	17.4	16	6.5	27	9.9
Stephanomia bijuga	7	0.2	27	0.8	13	1.2	22	2.0	11	0.2	27	1.8
Chelophyes appendiculata	33	10.0	76	89.3	17	5.0	47	7.6	32	2.6	67	46.2
Diphyes dispar	22	14.7	48	44.1	0	0	0	0	0	0	3	0.4
Liriope tetraphylla	22	20.9	64	253.6	37	96.5	42	41.8	21	6.8	58	89.4
Rhopalonema velatum	7	0.6	46	30.3	7	0.3	28	4.1	5	0.3	33	18.2
Aglaura hemistoma	0	0	12	40.2	0	0	3	1.1	5	0.2	18	51.7

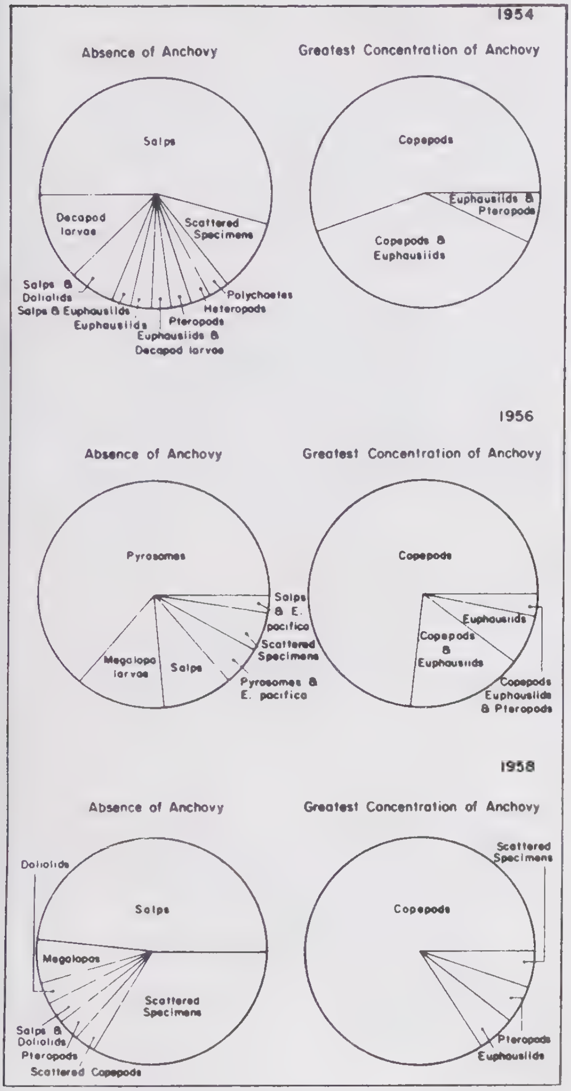

Figure 2. Relative abundance of various additional zooplankters at locations with highest concentration and absence of anchovy larvae, for 1954, 1956, 1958.

hauls with large concentration of anchovy larvae and in 4.95% of hauls with zero anchovy abundance. This could be interpreted as an indication that large concentrations of anchovy larvae occur infrequently in upwelling areas.

RELATION OF PLANKTON ASSEMBLAGES TO ANCHOVY LARVAE

During the 3 years Copepods were the dominant zooplankton group in samples rich in anchovy larvae. They dominated in almost 80% of those collections and in the remainder the dominant groups were Euphausiids and Pteropods.

In contrast, these groups were not dominant in hauls from localities with no anchovy larvae. In 1954 and 1958 the absence of anchovy larvae coincided in about 60% of the samples with dominance of Salps, and in other instances with Doliolids, Decapod larvae, Polychaetes, Pteropods and Euphausiids. In 1956 the dominant group in hauls lacking anchovy larvae were Pyrosomes, in more than 63% of hauls; while Megalops, Salps, and *Euphausia pacifica* dominated in other locations. The contrast in the major additional plankton constituents between anchovy rich and anchovy lacking hauls is striking (Fig. 2). This unanticipated finding indicates that anchovy larvae occur in abundance primarily in hauls dominated by Copepoda and/or Euphausiids, and never in hauls dominated by pelagic Prochordates. The former habitat can be characterized as "anchovy water". This fact also illustrates that predatory pressure of zooplankters is weaker when there is abundance of Copepods, which was also evidenced by the gut content analysis of those zooplankters.

In a recent colloquium dealing with larval fish mortality studies, it was concluded that "major causes of larval mortality are starvation and predation, and these may interact" (Hunter, 1976). Obviously, mortality from starvation is reduced when anchovy larvae are situated in waters with an adequate food supply, and mortality from predation is reduced when potential predators are in reduced abundance. This favourable combination of factors has been shown for "anchovy water".

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SPADELLA LEGAZPICHESSI, A NEW BENTHIC CHAETOGNATH FROM ENEWETAK, MARSHALL ISLANDS

Angeles Alvariño

Abstract.—*Spadella legazpichessi* is described from adult mature individuals and compared with related species, *S. schizoptera*, *S. moretonensis*, *S. johnstoni*, *S. sheardi*, *S. nana*, *S. pulchella*, *S. hummelincki*, with which it agrees in the presence of adhesive digital organs. The diagnostic characteristics of these species and *S. legazpichessi* are compiled in a table together with information on their geographical distribution.

Spadella is a genus of Chaetognatha including animals of benthic regimen. These animals are small, from less than 1 mm to less than 1 cm. Their restricted habitat and movements limit the distribution of the species. Specimens of *Spadella* do not appear in the usual plankton collections, and collectors of benthic animals usually overlook these small organisms. Therefore, they are obtained only occasionally. Up to now the number of species is one dozen, but I am sure that with proper sampling along the coastal regions of the world, many new species will be found, and a more adequate distributional range of all the known species of *Spadella* will be obtained.

Alvariño (1970) reviewed the geographic distribution of the species. Since then two more species of *Spadella* have been described, *Spadella bradshawi* Bieri, 1974 and *Spadella gaetanoi* Alvariño 1978, inhabiting California and the Hawaiian Islands, respectively. Also, *S. angulata* was observed at the Laccadive Islands (Nair and Rao, 1973). Now specimens of a new *Spadella* have been collected at the lagoon of Enewetak (formerly Eniwetok), Marshall Islands.

The new species of *Spadella* described here is related to *S. schizoptera*, *S. moretonensis*, *S. johnstoni*, *S. sheardi*, *S. nana*, *S. pulchella*, *S. hummelincki*, in the presence of adhesive digital organs on the ventrolateral sides of the tail segment. However, *S. schizoptera*, *S. johnstoni*, and *S. sheardi* have been described with two pairs of lateral fins, while *S. moretonensis*, *S. nana*, *S. pulchella*, and *S. hummelincki* have only one pair of lateral fins. Intestinal diverticula are absent in these species and in *Spadella* n. sp., although Yosii and Tokioka (1939) indicated they were present in *S. schizoptera*, where they are absent according to Conant (1895), Ritter-Zahony (1911), Mawson (1944). Probably the specimens analyzed by Yosii and Tokioka (1939) do not belong to *S. schizoptera*.

Spadella legazpichessi new species
Figs. 1, 2

Material.—Holotype (USNM No. 60191), paratypes (USNM No. 60192) collected at Enewetak atoll lagoon, Marshall Islands, in May 1979.

Diagnosis.—The anatomical features described here are based on mature adult specimens.

The body is opaque, with well developed muscles on the dorsal and ventral sides. Lateral sides very narrow. The whole animal presents a peculiar iridescence characteristic of most Chaetognatha. No pigment or pigmentation patterns have been observed (Fig. 1A, B).

Total length when mature, up to 2 mm, tail fin not included. The body is widest at the region of the transverse septum separating trunk and tail segments.

The head is large, strong, about the same length and width, but wider than the neck. It is about 13% of the total length of the animal. The neck is distinct and covered by a thick collarette (Fig. 2A).

The caudal segment constitutes 50% of the total length of the animal.

The eyes are large, oval, placed at center of dorsal side of the head, and at about the same distance from each other or slightly closer to each other than to the sides of the head. The pigmented region is large, formed by 2 branches; the longer extending parallel to the longitudinal axis of the body and curving laterally at each end; it is crossed at midlength by a short, thick, bifurcated transverse branch that runs medially. The pattern of the pigment in the eyes of *Spadella legazpichessi* is similar to that found in most species of *Spadella*. The pigment separates 3 large and one small clear amber spaces, filled by lenses. The bifurcation of the transverse branch of pigment is at times quite deep (Fig. 2A).

The hooks are strong, thick, strongly curved, as in *Sagitta ferox* and *S. robusta*, usually a group of 8 or 9 at each side of the head. The anterior teeth are 3 to 5 per set, long curved inward and posteriorly. The second and third teeth at each side, counting from the center of the head, are longer than the others, the third being the longest; the fifth is the shortest. No posterior sets of teeth were observed.

The corona ciliata is ring-shaped, with the transverse axis slightly longer than the longitudinal axis. It is located at the dorsal side of the neck, extending into the collarette region of the neck (Figs. 1A and 2A).

The collarette extends in a thick stratum from the head to level of posterior septum. It is thickest at the neck, tapering towards the posterior part of the trunk, and extending as a narrow stratum to the tip of the tail.

Intestinal diverticula absent.

The ventral ganglion is large, thick, occupying totally the width of the

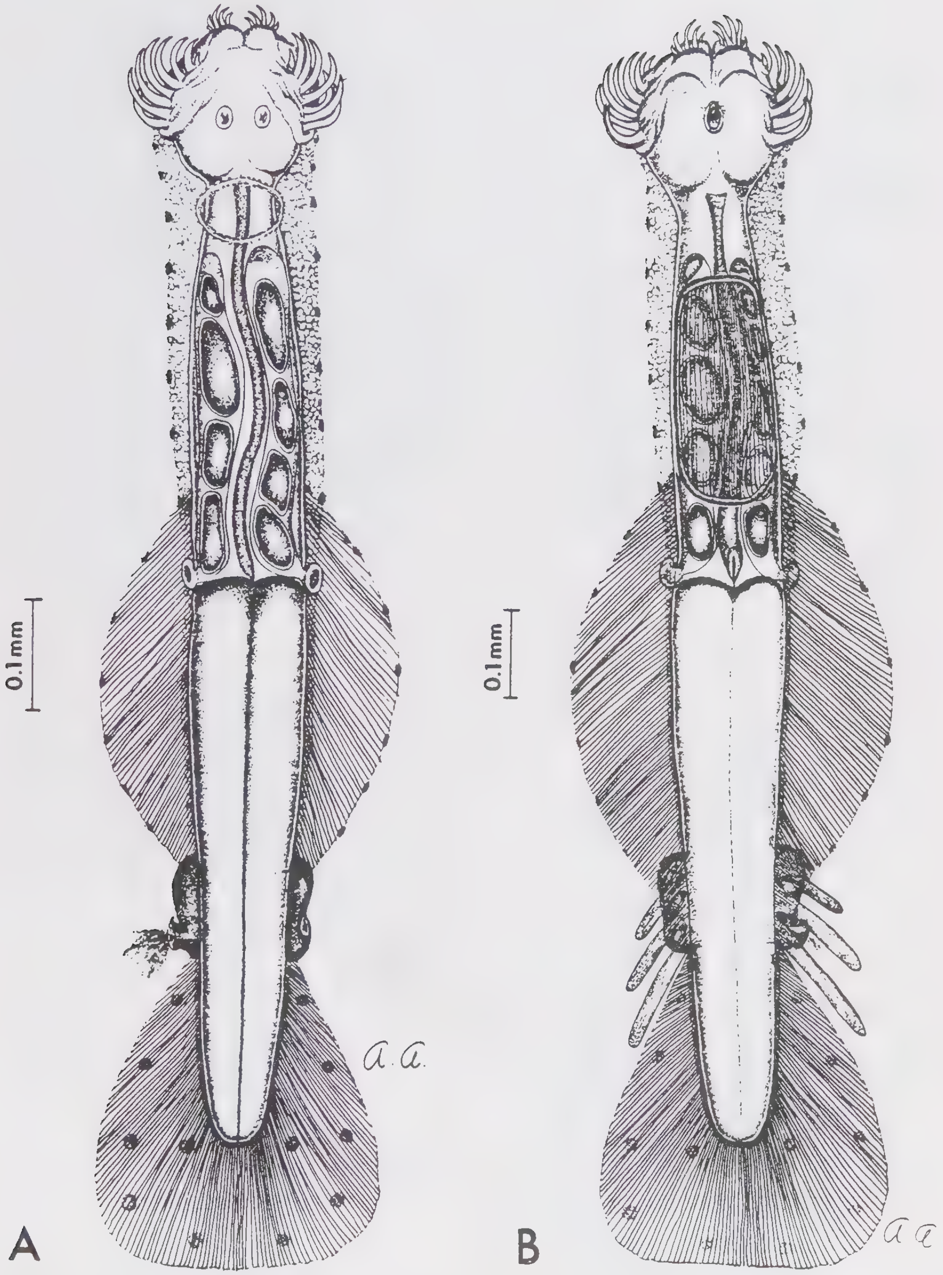

Fig. 1. *Spadella legazpichessi:* A, Dorsal view; B, Ventral view.

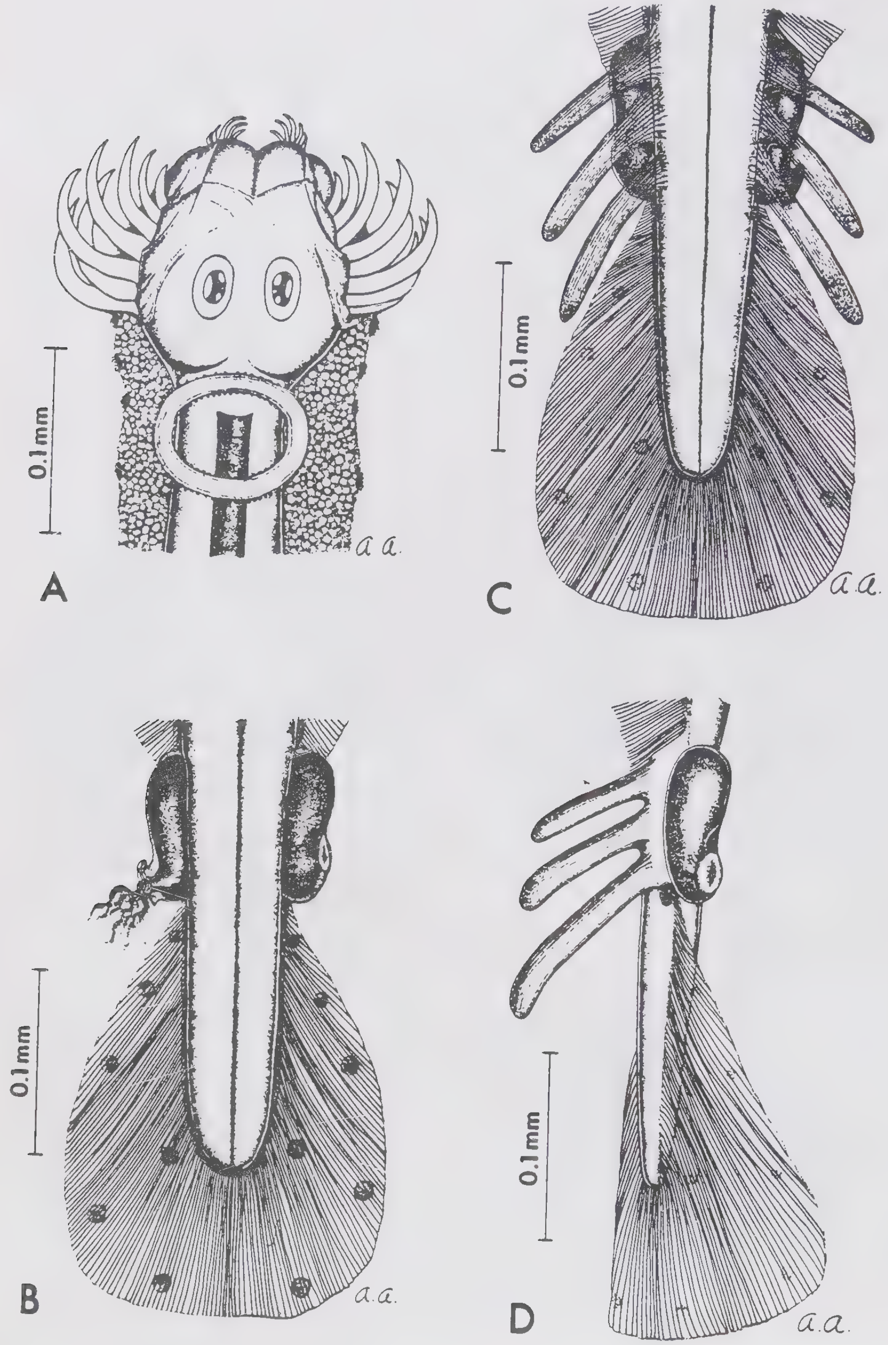

Fig. 2. *Spadella legazpichessi:* A, Dorsal view of head, with detail of hooks, teeth, eyes, corona ciliata, neck, collarette, and anterior part of intestine; B, Dorsal view of posterior part

trunk and half the length of the trunk segment. It is located at midlength of the trunk, as close to the neck as to the posterior septum (Fig. 1B).

There is one pair of lateral fins, extending from a level on the trunk anterior to the opening of the oviducts, to the seminal vesicles. They are completely rayed. The caudal fin is long, spatula-shaped, rounded laterally along the tip of the tail segment, with a straight posterior edge. It is not continuous with the lateral fins, and starts at posterior edge of the seminal vesicles. The portion of the tail segment surrounded by the tail fin is about 16% of the total length of the animal (Fig. 1A, B).

Adhesive digital organs are formed by three long rigid finger-like processes covered by a few small thin papillae. They extend along the ventrolateral side of the tail segment. The most anterior finger-like structure has part of the anterior edge joined to the posterior edge of the lateral fins, but the other 2 fingers are free. The posterior finger is the longest, and the anterior one is the shortest. The adhesive organs are at the ventrolateral side of the tail segment, exactly at the level of the seminal vesicles. Thus in the tail segment the seminal vesicles are dorsolateral, while the adhesive organs are ventrolateral (Fig. 2C, D). The adhesive organs are strengthened by long thin rays or muscle-like fibers, similar to the fin rays. The tip of the longest finger when extended, reached half-way between the seminal vesicles and the tip of the tail segment. These finger-like organs extend ventrally to support the animal away from the substratum while crawling, or to help in fastening the animal strongly to the substratum during the crawling motion, while the fins are used during the darting and swimming activities. In the dozens of specimens analyzed no variability was observed in the adhesive digital organs, such as that found by Feigenbaum (1976) in *S. schizoptera* reared in the laboratory. Such variability might be an artifact of the culture environment, not occurring in nature. However, adhesive organs in young specimens are not fully developed, the anterior finger appears first and the other two at each side of the animal are already incipient.

A cup-like structure is located ventrally at each side of the tail between the origin of the tail fin and the seminal vesicles. These cups may have additional adhesive function from the papillae covering the cup process and the secreted mucus (Fig. 2C, D).

The ovaries extend to the neck region. The ova are few and large, and they press laterally against the intestine, which usually runs in an S-shape

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of tail segment, with detail of seminal vesicles and tail fin. The left seminal vesicle is bursting; C, Ventral view of posterior part of tail segment, with detail of seminal vesicles, adhesive digital organs, and tail fin; D, Left side view of posterior part of tail segment, showing the dorsolateral position of seminal vesicles, and ventrolateral position of adhesive digital organs.

Table 1.—Differential characteristics of mature adult species of *Spadella* with digital adhesive organs.

Species Charact.	*S. schizoptera* Conant 1895	*S. moretonensis* Johnston and Taylor 1919	*S. johnstoni* Mawson 1944	*S. sheardi* Mawson 1944
Body length (mm)	1.9–4.9; wider at level of posterior septum	3.68	4.6; slender, yellow with brownish spots on corona ciliata	3.9–6.5; opaque, mauve brownish pigment along 3 longitudinal and 2 transverse bands. At level of oviducts, yellow spots on body.
Head	Broader than body with narrow neck. A pair of pads at mouth.	Broader than long. Neck conspicuous.		
Tail segment % to total length	47.0–53.7	56.5; two club-shape papillate bodies on posterior part of ventral side	52.0	44.8
Lateral paired fins	2 pairs; anterior pair extending from a point slightly behind the ventral ganglion to opening of oviducts. The second pair from this point to seminal vesicles.	1 pair, from oviducts to tail fin. Completely rayed and covered with sensory spots.	Similar to *S. schizoptera*	2 pairs; anterior short, on trunk. Posterior from opening of oviducts to seminal vesicles.

Table 1.—Continued.

S. nana Owre 1963	*S. pulchella* Owre 1963	*S. hummelincki* Alvariño 1970	*S. legazpichessi* Alvariño n. sp.
0.75–2.40	1.9–2.7; clusters of redish cells at anal region	2.0–3.0; broadest at the trunk	1.8–2.2; thick, strong, opaque, widest at mid-length.
Broader than widest part of body. Neck distinct. A pair of papillae between anterior teeth and mouth	Slightly broader than widest part of trunk. Neck distinct. A pair of prominences as in *S. nana* but with fewer papillae.	Large, roundish; smaller than in *S. pulchella*. Neck thick but distinct.	Large, roundish. Neck well distinct.
40–50	52–55	49	50
1 pair; from a level anterior to opening of oviducts to seminal vesicles.	1 pair; from a point anterior but close to oviducts to seminal vesicles extending ventrally over seminal vesicles joining tail fin	1 pair, long, narrow, from level anterior to opening of oviducts to seminal vesicles extending ventrally over seminal vesicles joining tail fin	1 pair, extending from posterior part of trunk to seminal vesicles.

Table 1.—Continued.

Charact. / Species	*S. schizoptera* Conant 1895	*S. moretonensis* Johnston and Taylor 1919	*S. johnstoni* Mawson 1944	*S. sheardi* Mawson 1944
Caudal fin	Long, spatula shape	Spatula shape, completely rayed, covered with sensory spots.		Spatula shape
Eyes		Large, with no pigment		Small, widely spaced and overlain by brown pigment
Hooks	8–11, long, curved. Points sharp	9, slightly curved like in *E. hamata*	10–11	Up to 11
Anterior teeth	2–3 long, slender curved towards the midline where they meet.	3–4, stout, curved.	2, long, about half length of hooks.	3, long, about ⅓ to ½ length of hooks.
Posterior teeth	None	None	None	None
Corona ciliata	Three corned shape or pear-shaped to roughly triangular. Part on head and part on neck.	Roughly elliptical, slightly pointed at anterior end.	Elliptical-rectangular, mainly on neck.	Triangular
Ventral ganglion	Large, thick, overlaid by numerous sensory spots.	Large at anterior half of trunk.		

Table 1.—Continued.

S. nana Owre 1963	*S. pulchella* Owre 1963	*S. hummelincki* Alvariño 1970	*S. legazpichessi* Alvariño n. sp.
Spatula shape, starting at posterior end of seminal vesicles	Spatula shape starting at a distance of posterior end of seminal vesicles. This distance is equal to the length of the vesicle.	Long spatulated shape, starting at a distance of posterior end of seminal vesicles equal to half the length of the vesicle. No rayless zone.	Spatulate in shape, starting at posterior end of seminal vesicles. Covered by 12 sensorial spots. No rayless zone.
	The pigment in a longitudinal band crossed by a short band at the center.	Large, roundish. Larger than in *S. pulchella*. Pigment in a thick X-shape.	Large, oval. Pigment in a longitudinal band tilted towards the sides, and at midlength a short band towards the center
5–9	8–10	8–9 each side. Slender, slightly curved.	8–9 at each side. Strong, curved like in *S. ferox*
1–3, the innermost longer than the others. Curved towards the midline.	2–4, long, slender, curved.	4 at each side. Long, thin, bent at about midlength.	Up to 5 at each side. First 3 longer than the others. The 3rd at each side is the longest. Curved towards the ventral side.
None	None	None	None
Variable in shape. Located at the neck extending towards the head.	Broad, irregular oval, located at neck and extending towards the head.	On neck, roundish with peak towards center of head.	Like a ring at dorsal part of neck.
As broad as long.	Large, midway between posterior edge of corona ciliata and posterior septum.	Large, thick, about half length of trunk, and almost as wide as trunk. Closer to posterior septum than to neck.	Large, thick at midlength of trunk, and about 50% length of trunk. As close to neck as to posterior septum.

Table 1.—Continued.

Species Charact.	*S. schizoptera* Conant 1895	*S. moretonensis* Johnston and Taylor 1919	*S. johnstoni* Mawson 1944	*S. sheardi* Mawson 1944
Sensorial spots	Abundant, extending on longitudinal and transverse rows.	On tail fin, lateral fins, sides of body and head.	Arranged in two symmetric groups along the body.	
Ovaries	Reaching neck or anterior end of ventral ganglion or its midlength.	Reaching to level of ventral ganglion. Few large ova. Opening of oviducts swollen and trilobed.		Up to neck. Open at clear space between posterior end of anterior fin and anterior end of posterior fin.
Seminal vesicles	Ellipsoidal, reniform, touching both lateral and tail fins.	Small, inconspicuous, on posterior third of tail segment.	Oval, yellow in color in living specimens.	
Intestinal diverticula	Present or absent (1)		Absent	
Adhesive organs	Hand shaped, prolongation of lateral fins with 4, 5, 6 finger-like processes, extending from posterior end of lateral fins. First finger longest and outmost shortest. All	Rudimentary.	At ventral side of seminal vesicles, extending over length of tail fin.	Laterally at ventral side tail between posterior fins and seminal vesicles, arranged in 2 groups at each side, one towards the anterior part of the animal and other towards the end. 10–11

Table 1.—Continued.

S. nana Owre 1963	*S. pulchella* Owre 1963	*S. hummelincki* Alvariño 1970	*S. legazpichessi* Alvariño n. sp.
Arranged symmetrically in pairs on caudal fin and longitudinal rows on the body.	Arranged symmetrically as in *S. nana*. Lateral spots on outer edges of collarette and lateral fins are conspicuous.	Numerous	Symmetrically arranged on tail fin (6 at each side) and 6 conspicuous along edge of lateral fins and more than 6 at each side along edges of collarette.
Reaching to neck. 2–5 huge ova and intestine is pushed into an S-shape.	Up to midlength of trunk, 2–3 large ova.	Reach to neck or anterior end of ventral ganglion. Few large ova.	Reach neck region. Few large ova, pushing intestine into an S-shape.
Oval, roundish anterior to tail fin. Protected ventrally by prolongations of lateral and tail fins.	Oval, extending from posterior end of lateral fins to adhesive organs.	Oval or pear shaped, touching posterior end of lateral fins to the adhesive organs and apart from tail fin. Open by lateral dorsal slit at about midlength.	Ellipsoidal, reniform, touching posterior end of lateral fins and anterior end of tail fin. Open at middle of edge towards posterior half of vesicle.
Absent	Absent	Absent	Absent
Extending ventrally from posterior end of lateral fins to seminal vesicles. Divided in 2 stout distally tubercular fingers, with muscular fibers. First finger is longest. In small specimens, only one finger per organ.	Extending from posterior end of seminal vesicles to the point the caudal fin starts. Not associated with lateral fins, not attached to caudal fin. 2–3 fingers in each organ. The innermost finger longer, slender, undivided; the	One hand shaped at each side, with 3 short, thick stout fingers each covered by thin papillae. Appear as extension of lateral fins, strengthened by ray-like pattern, continuation of the lateral fins and rising from latero-ventral	Three long thin fingers in each organ, prolongations of posterior end of lateral fins, but attached also at latero-ventral part of tail at level of seminal vesicles only. Not attached to tail fin. Outermost finger

Table 1.—Continued.

Species / Charact.	*S. schizoptera* Conant 1895	*S. moretonensis* Johnston and Taylor 1919	*S. johnstoni* Mawson 1944	*S. sheardi* Mawson 1944
	have adhesive papillae. A sensory spot at base of outermost branch.			fingers on each side, covered with papillae.
Collarette	Thick at neck, extending along base of lateral fins to seminal vesicles.	Thick at neck reaching lateral fins. Thus neck appears wider than the head.		
Geographic distribution	Bahamas, Florida, New South Wales? Misaki (Japan)?	Queensland	New South Wales	New South Wales.

(1) Characteristic varies with authors (see Alvariño, 1970).

from neck to anus. The opening of the oviducts are dorsolateral cups with an outer rim. The lateral fins extend ventrally anterior to the openings of the oviducts. The ventral disposition of the fins and dorsal placement of oviducts constitute a protective functional device to help in the transference of sperm during the copulatory process.

The seminal vesicles touch both posterior end of lateral fins and anterior end of caudal fin. They are large, reniform, about 8% of the total length of the animal. They open at the dorsal side by a dorsolateral slit in the posterior half, just beyond the midlength of the vesicle. This opening protrudes toward the posterior part in a short bottle neck, which adapts to the opening of the oviducts (Fig. 2B, D).

The sensory spots appear distributed on the tail fin, and along the edges

Table 1.—Continued.

S. nana Owre 1963	*S. pulchella* Owre 1963	*S. hummelincki* Alvariño 1970	*S. legazpichessi* Alvariño n. sp.
	other may split at the tip. Abundant papillae cover tip of 2 or 3 digitations.	side of tail segment between posterior end of seminal vesicles and start of tail fin. Attached by a point at tail fin, at the sensory club.	is the longest, reaching midlength from vesicle to tip of tail. Fingers strengthened by thin muscular fibers. Large sensory club on ventral side of tail at posterior end of seminal vesicles.
Thick at neck, tapering progressively towards the seminal vesicles. At head appears continuous with hood.	Very thick at neck and anterior part of trunk, extending along base of lateral fins to posterior septum.	Wide, thick, extending from head to posterior septum, widest at anterior half of trunk.	Thick at neck extending along lateral part of trunk, tapering towards posterior part of tail segment.
Florida	Puerto Rico	Southwest of Bahia Fosforescente, Puerto Rico	Enewetak (Marshall Islands)

of the lateral fins and edges of the collarette, from the head to the posterior part of the trunk. In the tail fin are 6 at each side, 6 along the edge of each lateral fin, and more than 6 along the edge of the collarette, from the point the collarette joins the anterior edge of the lateral fins to the head.

Remarks.—*Spadella legazpichessi* differs from *S. schizoptera*, *S. johnstoni*, *S. sheardi* in many anatomical characters, especially in the number of lateral fins, from *S. schizoptera* probably also in the intestinal diverticula, and from *S. moretonensis*, *S. nana*, *S. pulchella*, and *S. hummelincki* mainly in the shape of hooks, head, characteristics of the adhesive organs, position of ventral ganglion, and position of seminal vesicles (Table 1).

Distribution.—The specimens studied were collected at Enewetak atoll, Marshall Islands, on sand, rubble coral, and living coral. The collections were obtained with a bottom emergence trap for epibenthic and hypopelagic organisms, during studies on benthic marine communities. In those collections were also trapped pelagic species of Chaetognatha, *Sagitta ferox, S. robusta, S. neglecta, S. oceania,* which might be swimming and feeding in the water stratum over the bottom.

Etymology.—Named after the navigator Miguel López de Legazpi, whose party discovered the Marshall Islands in 1565, then named "Islands of Bearded people," and James R. (Tony) Chess, who kindly provided me with the material for this study. Legazpi's expedition reached those islands and atolls with four sailing vessels under Legazpi's Command (*San Pedro, San Pablo, San Juan* and *San Lucas*) departing from Navidad port (north of Acapulco) on November 1564 and reaching those islands, coral reefs, and atolls in January 1565, in their route to the Philippines. Legazpi's expedition constitutes the initiation of the first round trip across the Pacific, inaugurating with their return from the Philippines to Acapulco, the first regular transoceanic route, which also lasted longest in history, 1564 to 1815 (Colección de Diarios y Relaciones para la Historia de los Viajes y Descubrimientos).

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NEW RECORDS OF *ALLOPOSUS MOLLIS* VERRILL (CEPHALOPODA, OCTOPODA) FROM THE PACIFIC OCEAN

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ABSTRACT

Two specimens of Alloposus mollis *(Alloposidae) captured off southern California are described and illustrated. The anatomical characteristics of the species are discussed, and its distribution is reviewed.*

Alloposus mollis is a relative rarely captured mesopelagic cephalopod. Records of this species are few and locations scattered. The published illustrations and descriptions are rather incomplete and diagrammatic because of the lack of specimens in good condition of preservation.

Verrill (1880) originally described the species from specimens collected off New England in the North Atlantic. Additional specimens were reported by Verrill (1881) and Hoyle (1886) from off Newport, Rhode Island, the mouth of the Chesapeake Bay, and in other parts of the Atlantic (Joubin, 1895, 1900; Robson, 1930 for his *A. hardyi*; Thore, 1949; Adam, 1960). Ijima and Ikeda (1902) described an allied species, *A. pacificus,* from the Sagami Sea, Japan, and this species was recorded also for Sagami Bay, Japan, by Sasaki (1929). Berry (1914) suggested that the evidence was not sufficient to warrant two different species. Similarly, *A. hardyi* is believed to be synonymous with *A. mollis* (Thore, 1949). Specimens belonging to the family Alloposidae obtained at Pailolo Channel, Hawaii and other ALBATROSS stations in the Pacific (Hoyle, 1904; Berry, 1914) were considered to belong to *A. mollis.* Alloposidae material from the DANA collections, including specimens from the Atlantic, Indo-Pacific (05°52′N, 131°14′E) and the Indian Ocean (04°52′N, 77°08′E), were placed by Thore (1949) under *A. mollis.* Young (1972) obtained one specimen from Santa Catalina Basin, California (33°23′N, 118°49′W). This specimen, judging from the illustrations, was not complete and in bad condition of preservation, facts also explained by Young (1972) when he comments "... very large, but rather poorly preserved specimen".

Two specimens of *A. mollis* in excellent condition were taken off the southern California coast during survey cruises conducted by the National Marine Fisheries Service's R/V DAVID STARR JORDAN. These records together with the one by Young (1972) are the first reported specimens obtained from the North American Pacific. This report documents these records, provides a description and illustration of the specimens and review, the distribution and external morphology of the species.

Alloposus mollis Verrill, 1880

Material examined–The specimens collected were: Specimen A (200 mm total length, head and mantle) captured July 18, 1976 (2349 hours PST) at 33°23′N, 117°43′W in a six feet Isaacs-Kidd midwater trawl towed to a maximum depth of 70 m; and Specimen B (67 mm total length, head and mantle to base of arms) collected March 24, 1977 (0410 hours PST) at 33°31.8′N, 117°58′W, in a midwater trawl towed at a maximum depth of 7 m. Both specimens were females.

Description–These animals are ovoid in shape, widest at the head region. They are soft and of smooth gelatinous consistency, translucent, and covered with small red spots, giving the whole animal a brick-purple color. The head is large, short and slightly broader than the body. The mantle opening is wide and full, and in two broad pouches, extending dorsally from

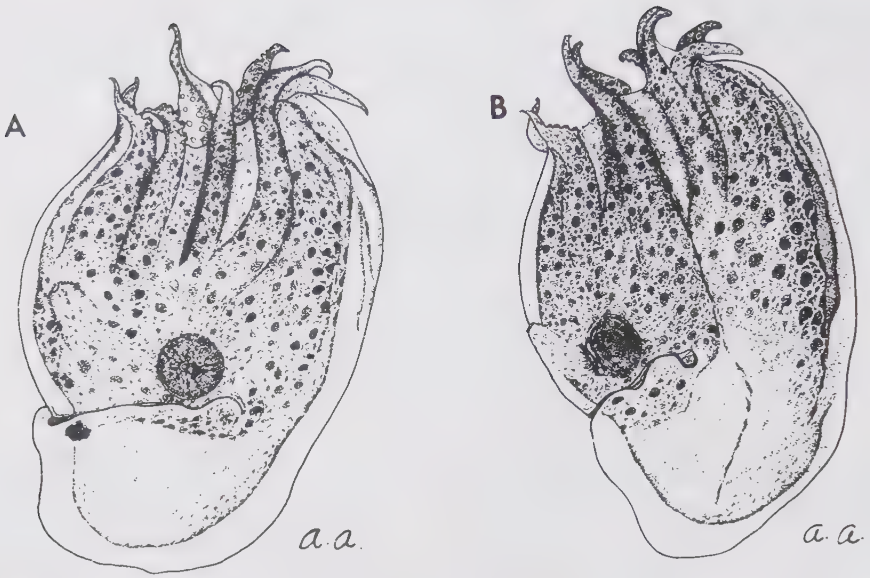

FIG. 1. **A**–*Lateral left view of* Alloposus mollis *(Specimen B);* **B**–*Dorso lateral left view of* Alloposus mollis *(Specimen B).*

the ventral point of the commissure towards the level of the eyes (Fig. 1). The eyes are large and prominent, covered by the eye lid. The lid has a small central opening which can be expanded to expose the entire eye (Figs. 2A and 2B). The funnel is large and is embedded with the gelatinous tissue of the head, except for the top which is free, reaching to a level higher than the upper edge of the eyes. The olfactory organ, a flat round lump, is located posteriorly to the eyes.

The arms are stout and short, relative to the body length (head and mantle), and they decrease in length from the dorsal to the ventral side. They are connected at the base by a broad membrane, web or umbrella, which attains the greatest extension between the dorsal pair of arms. The suckers are arranged in a straight row of 3 to 4 (ventral arms) or 4 to 6 (dorsal arms), from the mouth to the point on the arm where the web starts. At this point the suckers begin to deviate from a straight course to an incipient zig zag arrangement, which becomes more evident along the webbed and the free part of the arms (Fig. 2C). This pattern occurs in both specimens we collected, in Verrill's syntype, and in all other specimens we received from the Division of Mollusks at the Smithsonian Institution, which included the material examined by Berry (1914). Measurements from our specimens are given in Table 1.

Discussion–The arrangement of the suckers on the arms is an important character and subject to some disagreement and confusion in the literature. Ijima and Ikeda (1902) described an allied species, *A. pacificus,* from the Sagami Sea, subsequently reported by Sasaki (1929) from the same body of water in the Sagami Bay, Japan. Berry (1914) stated that the anatomical differences between *A. pacificus* and *A. mollis* were insufficient to establish a new species. According to Ijima and Ikeda (1902) the suckers of *A. pacificus* were arranged in a single row for most of the length of the arm, and were biserially arranged only on the free part of the arm, that is, from the edge of the web to the outer tip of the arm. This same characteristic was mentioned by Robson (1930) for *A. hardyi.* Verrill (1880) specifies that the suckers are "large, single, in two alternating rows," and Verrill

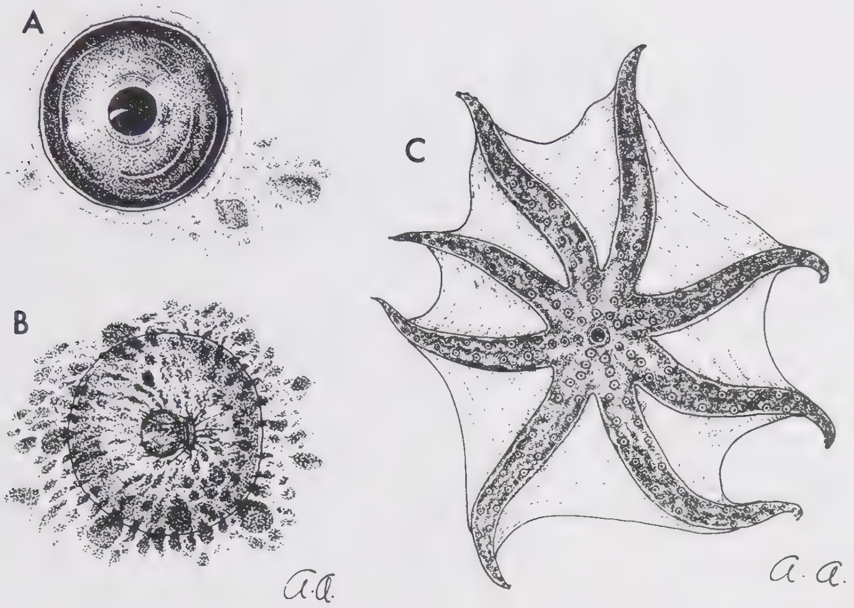

FIG. 2. **A**–*Eye with the eyelid expanded, exposing the eye (Specimen A);* **B**–*Right eye with sphincter of eyelid contracted; the diameter of the opening corresponds to that of the pupil of the eye (Specimen B);* **C**–*Detail of the crown of arms and interarms web, and the disposition of the suckers of female* Alloposus mollis *(from both Specimen A and Specimen B).*

(1881) states that the suckers "are in two rows or rather in a single more or less zig zag row which most conspicuously approached the two rowed condition after reaching the margin of the umbrella (at about the 13th sucker on the dorsal arms)." Robson (1930) explained for *A. hardyi* that "suckers tend to be uniserial or very widely alternating except about or just beyond the margin of the web, where they are more or less biserial." The suckers in our specimens are arranged, as explained above, in a straight row from the mouth to the point where the web starts, and at this point the suckers initiate an incipient zig zag arrangement, which becomes clearly evident along the webbed and free part of the arms (Fig. 2C). The suckers are 1 to 12 mm in diameter and their number varies from 12 (Thore, 1949) to 155 per arm (Joubin, 1900).

The proportions of the body in *A. mollis* change slightly with age; older specimens have relatively shorter bodies and longer arms than young individuals.

The only sexual dimorphism in Alloposidae is the third right arm, hectotylus of males. The males have 7 normal arms and the hectotylized arm. Verrill (1881) reported a hectotylus reaching 200 mm in length and 20 mm in width, with two rows of large 4-mm diameter, 6 or 7 lobed suckers, with a terminal process 30 mm long and 7 mm diameter.

Most of the specimens of *A. mollis* obtained by other authors were partially destroyed, injured during trawling, or only fragments of large individuals. Our specimens were alive and in excellent condition when brought on deck, and the morphological structures were accurately maintained (Fig. 3). No dissections were made to examine the internal atatomy or stomach content, because we felt it was important to keep the specimens in good conditon.

TABLE 1. *Meristic data on the specimens of* Alloposus mollis *collected off California.*

<table>
<tr><th></th><th>Total length mm</th><th>Width mm</th><th>Head width mm</th><th>Length funnel mm</th><th>Eye diameter mm</th><th>Diameter open. eye lid mm</th><th>Width mantle mm</th><th>No. suckers mm</th><th>Size suckers mm</th></tr>
<tr><td>Specimen A</td><td>200</td><td>65</td><td>76</td><td>36</td><td>26</td><td>3</td><td>80</td><td>>80</td><td>3 to 1</td></tr>
<tr><td colspan="10">Total length of arms from ventral to dorsal</td></tr>
<tr><td></td><td></td><td>right</td><td>left</td><td colspan="6"></td></tr>
<tr><td></td><td>I</td><td>82</td><td>76</td><td colspan="6"></td></tr>
<tr><td></td><td>II</td><td>88</td><td>82</td><td colspan="6"></td></tr>
<tr><td></td><td>III</td><td>92</td><td>85</td><td colspan="6"></td></tr>
<tr><td></td><td>IV</td><td>120</td><td>117</td><td colspan="6"></td></tr>
<tr><td colspan="10">Length of free part of the arms</td></tr>
<tr><td></td><td></td><td>right</td><td>left</td><td colspan="6"></td></tr>
<tr><td></td><td>I</td><td>43</td><td>40</td><td colspan="6"></td></tr>
<tr><td></td><td>II</td><td>40</td><td>37</td><td colspan="6"></td></tr>
<tr><td></td><td>III</td><td>52</td><td>50</td><td colspan="6"></td></tr>
<tr><td></td><td>IV</td><td>85</td><td>82</td><td colspan="6"></td></tr>
<tr><td>Specimen B</td><td>67</td><td>38</td><td>40</td><td>16</td><td>8</td><td>1</td><td>42</td><td>20-30</td><td>1.5 to <1</td></tr>
<tr><td colspan="10">Total length of arms from ventral to dorsal</td></tr>
<tr><td></td><td></td><td>right</td><td>left</td><td colspan="6"></td></tr>
<tr><td></td><td>I</td><td>24</td><td>20</td><td colspan="6"></td></tr>
<tr><td></td><td>II</td><td>35</td><td>32</td><td colspan="6"></td></tr>
<tr><td></td><td>III</td><td>36</td><td>34</td><td colspan="6"></td></tr>
<tr><td></td><td>IV</td><td>40</td><td>40</td><td colspan="6"></td></tr>
<tr><td colspan="10">Length of free part of the arms</td></tr>
<tr><td></td><td></td><td>right</td><td>left</td><td colspan="6"></td></tr>
<tr><td></td><td>I</td><td>12</td><td>10</td><td colspan="6"></td></tr>
<tr><td></td><td>II</td><td>15</td><td>15</td><td colspan="6"></td></tr>
<tr><td></td><td>III</td><td>18</td><td>17</td><td colspan="6"></td></tr>
<tr><td></td><td>IV</td><td>22</td><td>22</td><td colspan="6"></td></tr>
</table>

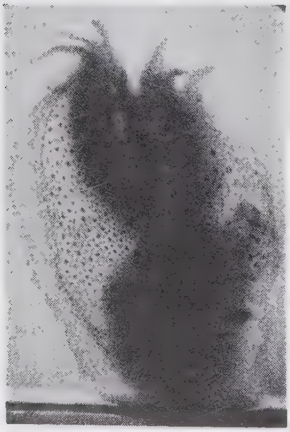

FIG. 3. Alloposus mollis *(Specimen B), length 67 mm.*

Distribution–Alloposus mollis is a cosmopolitan species, usually found near tropical and subtropical oceanic regions (Tables 2 and 3; Fig. 4). The majority of the deep-sea cephalopods were collected in trawls and probably are adept at avoiding nets of all types. The capture of our specimen B (Fig. 3) was observed by biologists on deck of vessel, and it was efficiently avoiding capture, when net was directly towed in pursuit of the specimen. Similarly, Thore (1949) suggested that *A. mollis* may only appear to be rare because of their ability to avoid capture. *A. mollis* may inhabit the open sea during certain phases of its life cycle, and remain in deep and bottom layers of the continental slope during other (Thore; 1949).

Our specimens were both juvenile females

TABLE 2. *Compilation of world data on* Alloposus mollis *Verrill.*

Location	Size	Length of body to base of arms	Mantle	Width of body	Head width mm	Length arms mm	Perim. arms mm	Number of suckers on: arm I	Number of suckers on: arm IV	Diam. suckers	Disposition of suckers on arms	Size of eyes	Sex	Depth	Temp. °C	Author
39°48'N, 70°50'W 39°46'N, 71°05'W 39°52'N, 70°58'W 39°56'N, 70°59'W 37°24'N, 74°17'W 38°21'N, 73°32'W		90 mm		70 mm		Dorsal 60 mm longer than ventral					Arranged in one or two rows.	Large				Verrill, 1880
100-150 miles south of Newport (Rhode Island)	160 mm	90 mm	50 mm	70 mm		70				7 mm	In one or two rows.					Verrill, 1881
38°52'N, 38°53'N - 69°24'W, 69°23'W																Verrill, 1884
North Atlantic																Hoyle, 1886
42°45'N, 22°16'W to 41°32'N, 43°20'W							70	60	132	12 mm						Joubin, 1895
37°55'N, 27°44'W and 38°04'N, 25°22'W						650 to 1610 mm		100	155							Joubin, 1900
Sagami Sea, Japan											In a single row or most part of arm and biserially arranged only on free tip					Ijima and Ikeda, 1902
00°19'N, 90°34'W																Hoyle, 1904
Pailolo Channel, Hawaii	147+	65 mm		46-51		51-82				4 mm	In 2 rows or rather in a single zig-zag pattern after reaching margin umbrella					Berry, 1914
00°56'W, 14°80'W			40 mm	35	38	50-112					Tend to uniserial or alternating, except, beyond margin of web, when adopt biserial pattern		M	0 m		Robson, 1930
16°06'N, 76°02'W	13		6		6.5	6.5		19	17	1.17				33	18°6C	
25°-35°N and 74°-45°W																
15°31'N, 18°05'W	29		11.9		30	15		17	14	1.2		10.8	M	33	"	
08°26'N, 15°11'W	44		18.9		41.8	22.8		17	12	2.3		14	M	33	"	
05°31'N, 18°05'W	52		20.8		49.4	31.2		25	17	2.5		17.1	M	33	"	
13°31'N, 18°03'W	60,70		22.8, 26.2		60,77	33, 43.1		25, 26	20	2.6, 4.5		21, 26.9	F	33	"	
37°23'N, 26°02'W 37°40'N, 26°00'W	91		34.6		91	59.1		30	25	5.4		36.4	M	333	9°16-11°39C	
05°52'S, 131°14'E	400		100		440	348				8		152	F	333	"	
04°52'N, 77°08'E													2 sps.			
27°10'N, 08°59'E													1 sp.			Thore, 1949
West of Saint Louis (Africa)			80-60					250+	220	5		35	M	800-650		Adam, 1960
Santa Catalina Basin (33°23'N, 118°49'W)			115	126	120	360-200						38	F			Young, 1972

TABLE 3. *Data on specimens from the Smithsonian Institution.*

Number of specimens	Total length mm	Position	Depth m	Date
1 male	120	39°52'N-70°58'W (off Rhode Island)	680	1880
1 *	60	Hawaiian Islands (Pailolo Channel)	530.4	22 July, 1902
4 males	variable	21°06'N-156°13'W (Hawaiian Islands)	686	5 April, 1968
1 *	120	21°01'N-156°43'W (Hawaiian Islands)	548.7	17 Nov., 1968
1 *	55	12°24'N-82°24'W (Caribbean Sea)	612.7	22 Nov., 1968
Several *	medium	28°17'N-86°21'W (Gulf of Mexico)	671	20 June, 1969
2 *	55	18°52'N-94°50'W (Gulf of Mexico)	612.7	5 June, 1970
1 *	large	24°24'N-87°49'W (Gulf of Mexico)	567	14 Aug., 1970
1 *	45	28°00'N-85°20'W (Gulf of Mexico)	521	27 Aug., 1970
1 *	88	29°46'N-88°25'W (Gulf of Mexico)	36.5	14 April, 1972

* Due to bad condition of preservation of specimens, sex could not be determined.

Total length includes head and mantle.

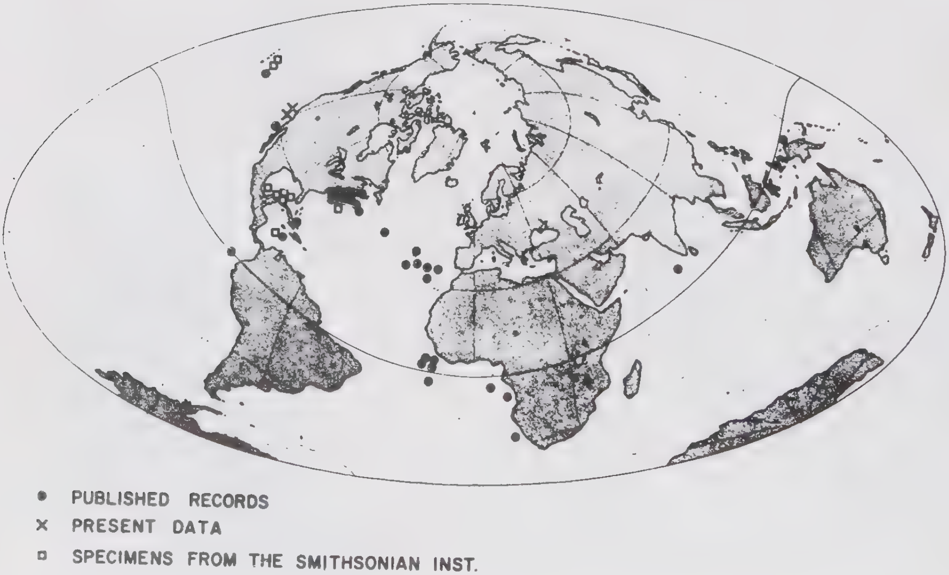

FIG. 4. *Distribution of* Alloposus mollis.

(200 mm and 67 mm in total length) and were taken at 70 m and 7 m depth respectively. According to Verrill (1881) the bathymetric range of the species extends to 2462 m depth, and fragments of specimens were taken from 3173 m depth. Berry (1914) states that it extends from 180 m to more than 900 m depth. Voss (1967) explains that Alloposidae appear to be distributed in the upper 400 m, although they may extend to more than 3000 m depth, and that larvae and juveniles occur in the upper 100 m.

Populations of *A. mollis* probably are stratified ontogenically, as is often the case in oceanic animals.

The temperature of the surface waters at the time of capture of our two specimens was 14.6°C (Specimen A), and 13.0°C (Specimen B), which is well within the range of temperature recorded for the species (Thore, 1949).

Cephalopods are important in the food web of the oceans, as they constitute the main food of dolphins, sperm whales, other sea mammals, turtles, Thunnidae, sharks and other large fish. Joubin (1895, 1900) found fragments of *A. mollis* (dorsal region and tentacular crown) in a region of the Atlantic where sperm whales were feeding, but found no *A. mollis* in their stomachs, possibly because of the difficulty in identifying digested gelatinous remains.

ACKNOWLEDGMENTS

We would like to extend our appreciation to Dr. Joseph Rosewater and Michael J. Sweeney, Division of Mollusks, Smithsonian Institution, for providing us for comparative analysis the syntype and good amount of material of *Alloposus mollis*. We are also grateful to Carol A. Kimbrell for obtaining Specimen A, here studied, from the trawl collections at the Southwest Fisheries Center, to Daniel L. Gittings (Librarian, SWFC) and Nelson Ross (NODC) for their great cooperation in providing us with valuable literature pertinent to this subject. We also like to thank Roy M. Allen for the preparation of the distributional map.

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COMPARISON OF VARIOUS SEA SURFACE TEMPERATURE FIELDS

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1. ABSTRACT

Different estimates of the monthly mean sea surface temperature (SST) fields are intercompared. Fields derived from ship data alone differ substantially in high SST gradient regions and in areas of low data density. These differences exhibit seasonal and interannual variations which are spatially correlated. The large bias and variability preclude interchangeable use of different SST products derived from ships alone.

The difference between SST fields from ships and similar fields derived from a blend of satellite and ship data show many of the characteristics noted above, north of 30°N. However, inclusion of satellite data results in a warm bias that is substantially larger than that found between ship-only products. The difference fields south of 30°N are of order one standard deviation or more with the blended product again generally being warmer. The difference fields are regional in nature at all latitudes. Thus global or zonal

averaging of the fields, as is done in many papers comparing satellite SST's with other estimates, could lead to erroneous conclusions regarding the degree of comparability between the fields.

2. INTRODUCTION

Knowledge of the oceans' surface temperature is valuable in a variety of areas of research. As a result, a number of different analyses are currently being made to give maps of sea surface temperature (SST). These maps are available at a variety of time intervals from daily through monthly averages. They cover different spatial scales from those associated with frontal zones to the global ocean.

In view of the proliferation of SST products, it seems important to determine if they are all providing the same basic information. For instance, Barnet et al (1979) showed large differences existed between in situ data and satellite derived SST in the central Tropical Pacific. To initiate a broader comparison we have concentrated on monthly mean SST products for the Atlantic and Pacific Oceans. The prime question we addressed was: Do different SST products give similar estimates of the temperature field over both space and time? If differences do occur, we will not attempt to say which SST product is correct, for indeed there is no way to know for sure. We will, however, contrast the differences where possible with natural interannual variability of SST to see if the differences are important for climate studies. Our primary purpose is to determine if there are potential problems in the SST products, not to do an extensive evaluation of them.

In the following section we compare SST fields developed from in situ data; mainly synoptic ship reports. These differences are then contrasted with those obtained by comparing a product derived by blending satellite and in situ measurements with one of the in situ-only products. The SST products were selected solely on the basis of being the most conveniently available for analysis given the time and resources available for this study.

3. SST PRODUCTS DERIVED FROM SHIP OBSERVATIONS

3.1 Temporal Comparison

Different methods of constructing SST products could possibly lead to rather large differences between them. To investigate this we subtracted monthly temperatures derived from the National Climatic Center's historical sea surface temperature (HSST) summary product, T_{HSST}, from the monthly product of the National Marine Fisheries Service (NMFS), Southwest Fisheries Center in La Jolla, California (T_{SWFC}). These two products are developed in very different ways. The HSST data were obtained by averaging all available data within large ocean areas to give a single SST value for each area/month. The data came from ships' logbook reports (TDF11). Clearly, shifts in the geographical distribution of reports within the regions can have an impact on the final monthly average, particularly if there are large natural SST gradients in the averaging area. The SWFC data were computed as simple averages over 5^{o} latitude/longitude squares. The input for the calculations was the radioed ship reports available over the global weather reporting network at synoptic periods. The 5^{o} SWFC data were summarized into Marsden Squares for direct comparison with T_{HSST} at several selected sites (Fig. 1, inset). The regions selected for comparison were either data rich and/or thought important to climate change.

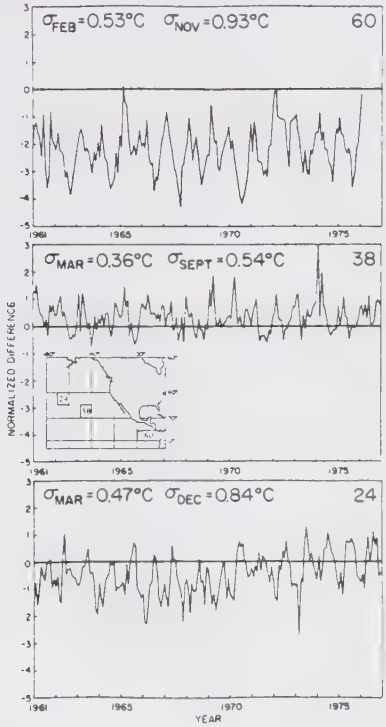

Fig. 1: The difference between sea surface temperature estimated by the National Marine Fisheries Service minus that estimated from the historical sea surface temperature project in key regions of the Pacific. The differences have been normalized by the standard deviation associated with the NMFS field. The inset of the middle panel shows the location of the regions. Their identification number is given in the upper right hand corner of each panel. The seasonal extremes in standard deviation associated with each region are indicated.

The difference ($T_{SWFC} - T_{HSST}$) was computed for each month between 1961-1976. Remember these are not anomalies but differences in actual SST. To put them into perspective, they were divided by the SWFC standard deviation of monthly SST (σ_{SWFC}). Thus the differences introduced by analysis methods can be directly related to a self-consistent measure of natural climatic fluctuations in SST.

The difference between the data sets is substantial. The region off Central Americal (Fig. 1, upper) shows a large bias between the two SST products of over two standard deviations ($>1.5^{o}C$). The scatter about this bias is also approximately $\pm 2\sigma$. The differences are largest in the early fall (typically October) and smallest in early spring (typically March). This seasonal signal in the difference field is roughly 2σ. Note that it is out of phase with the seasonal variations in standard deviation (Fig. 1, upper).

Region 38, on the data rich shipping lanes between the west coast and Hawaii, shows that a bias is still present but in the opposite sense (T_{SWFC} warmer) and smaller, roughly 0.5σ ($\sim 0.5^{o}C$). The seasonal character of the scatter persists and is roughly 1.5σ ($\sim 1^{o}C$). T_{SWFC} tends to be warmer than T_{HSST} in the late winter and spring but colder in late summer to early fall.

Region 24 shows many of the same properties as Regions 38 and 60. In addition there is a disturbing low frequency component in the temporal variability that one might mistakenly attribute to natural climatic fluctuations.

In summary, it is clear that the two data sets compared here have substantial temporal differences between them. Some of the problem was traced to shifts in the sampling centroids of the HSST set. The SST differences are as large or larger than typical natural variations that occur in the selected areas (according to any one data set). The differences have both annual and interannual time scales. Each data set, by itself, may be useful for climate studies but it is clear that the two data sets cannot be used either together or interchangeably without serious risk of faulty conclusion. A more complete discussion of the differences and similarities between the HSST and SWFC SST fields is given by Steiner

3.2 Spatial Comparison

This comparison involved two different products derived from virtually the same input data, the radioed synoptic ship reports. One might expect better agreement than obtained above from somewhat different, but still highly overlapping, data sets.

The first SST product came from the NMFS Pacific Environmental

Group (PEG). The radioed reports are obtained directly from the Fleet Numerical Oceanographic Center (FNOC) and made available to PEG where they are edited and then averaged by 1^{o} square. The 1^{o} averages are then averaged in 5^{o} boxes to obtain a 5^{o} temperature for each month (T_{PEG}). These values were compared with the FNOC product derived from virtually the same data and projected onto 63 x 63 grid spanning the Northern Hemisphere. A new FNOC analysis is developed every 12 hours by successive interpolation of the observed values, plus climatology in data poor areas. The monthly mean of the 12 hourly fields (T_{FNOC}), which was rather smooth, was projected onto the T_{PEG} 5^{o} grid, the differences ($T_{PEG} - T_{FNOC}$) computed and normalized by σ_{FNOC}, the standard deviation with respect to a long term monthly mean. Four January and four July difference fields were constructed in this manner.

Typical maps of $(T_{PEG} - T_{FNOC})/\sigma_{FNOC}$ are shown in Figure 2. Analysis of the January data showed that the largest discrepancies occur routinely in the following areas: 1) off the east coasts of the continents, where the strong SST gradients associated with the Gulf Stream, Kuroshio and their seaward extensions introduce tremendous sampling and analysis problems; differences of $1\sigma(\sim 2\text{-}3^{o}C)$

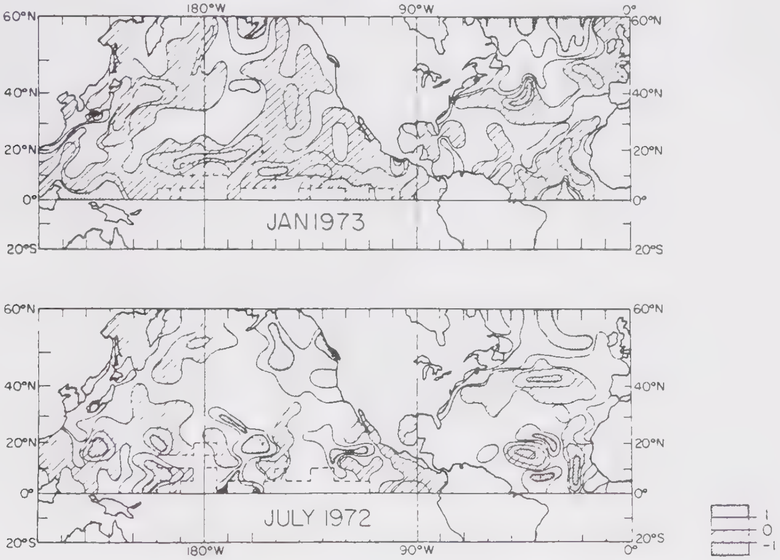

Fig. 2: SST fields from the Pacific Environmental Group minus the SST fields from the Fleet Naval Oceanographic Center. The differences have been normalized by the FNOC standard deviation and the results contoured at intervals of 0.5σ. These normalized difference fields, taken during periods of large SST anomaly, are typical of those found in other January and July's.

are common in these areas; 2) in the central and eastern portions of the Pacific below 20°N where the observation density is low, where $T_{FNOC} > T_{PEG}$ by roughly 0.5-1σ (0.5-1°C) suggesting, perhaps, the influence of climatology on the SST field; 3) off Newfoundland and Greenland, which are data poor areas, $T_{PEG} > T_{FNOC}$ by about 1-2σ(∿1°C); and 4) there is a general tendency for $T_{FNOC} > T_{PEG}$ in the Pacific, independent of position, while the reverse is true in the Atlantic. The value of the difference is about 0.5°C for both cases. The number of positive differences in the Atlantic is roughly twice the number of negative values, while in the Pacific the negatives outnumber the positives in approximately the same proportion. There seems no good explanation for this, unless it is again due to inclusion of climatology in the FNOC product.

During July most of the above conclusions hold. If anything, the magnitude of the differences in the areas noted in 1) and 3) are somewhat larger and show more year-to-year variability. Item 4, the general bias, still exists only now $T_{PEG} > T_{FNOC}$ in both oceans. The ratio of positive differences to negative is roughly 2 to 1.

In summary, different SST products derived from the same basic data set of ship reports differ from each other by amounts large relative to climatology in areas of high SST gradient (Gulf Stream, Kuroshio, etc.) and/or low observation density. In data rich areas the two sets agree much more closely but still tend to have a significant, though small, bias. The large differences, when they occur, are time dependent and tend to have large space scales similar to SST anomalies from any one data set. It is concluded, again, that different SST products, used interchangeably in climate studies, may introduce a high risk of erroneous results.

4. SATELLITE/SHIP DERIVED SST PRODUCTS

The blended satellite/ship SST product used in this section came from the National Meteorological Center (NMC) and spans the period April 1979 - January 1980. The data was available numerically on a 2° grid as monthly averages. Details of the construction of these fields may be obtained from Larson (personal communication). The analysis method has undergone changes over the above time period, as NMC strives to improve its analysis. The result of these changes will be evident below.

4.1 Temporal Comparison: Satellites vs. In Situ

A limited number of runs of the operational NMC global SST analysis system were made in which each in situ SST report (from ship injections, XBT's, fixed and/or drifting buoys) were compared to all TIROS-N retrievals falling within 50 km of its location and 3 days of the observation time. TIROS-N retrievals are provided by the National Environmental Satellite Service and consist of a temperature which is intended to be representative of a 50 x 50 km area. The center of the square is the position of the retrieval. The TIROS-N SST was subtracted from the in situ SST, the resulting differences were edited for gross errors and the remaining values summarized by latitude bands for each run. This zonal averaging process, which has often been used in previous satellite SST comparisons, is potentially a dangerous step as we shall see below.

Summaries of the comparisons by season for the latitude bands of 0° to 10°N and 45°N to 55°N are presented below. Table 1 shows the number of paired measurements and runs (in brackets) from which they were derived. Each run represents a different synoptic situation separated by at least a few days. Table 2 shows the differences between the satellite SST and the in situ observations summarized by seasons. An adequate climatology was not available to normalize these numbers by a standard deviation as in Section 2.

Table 1

Number of Paired In Situ/TIROS-N Reports and Runs (Parenthesis) From Which They Were Derived

0-10°N	Injection	XBT	Drifting Buoy	Fixed Buoy
Spring 1979	86(9)	24(2)	0	0
Summer 1979	324(9)	14(2)	45(7)	0
Fall 1979	396(13)	83(5)	101(8)	0
45°N-55°N				
Spring 1979	150(5)	60(7)	0	12(3)
Summer 1979	254(7)	28(2)	30(3)	9(4)

In the region 0 - 10°N, a warming of TIROS-N SST measurements relative to in situ observations occurred over the entire period studied. By fall, the initial positive mean difference of ∿1°C had decreased to nearly zero. This does not imply that by fall all satellite retrievals were correct -- only that the average bias had disappeared in this latitude band. Much of this change is thought due to changes by the National Environmental Satellite Service in the algorithm that is used to estimate SST from the raw satellite data.

In the band 45°N-55°N, TIROS-N retrievals were on the average slightly warmer (0.1°C) than co-located in situ measurement in the spring, but by summer this bias had increased substantially to ∿1°C. As at 0°-10°N, the various types of in situ data were quite consistent with the exception of a limited number of XBT/TIROS-N pairs collected during the summer. After early October satellite

Table 2

In Situ/Satellite Intercomparison

$0-10^{\circ}N$	Ship Mean (Std. Dev.) $^{\circ}C$	XBT Mean (Std. Dev.) $^{\circ}C$	Drifting Buoy Mean (Std. Dev.) $^{\circ}C$	Fixed Buoy Mean (Std. Dev.) $^{\circ}C$
Spring 1979	1.0 (1.3)	0.9 (0.6)	- -	- -
Summer 1979	0.6 (1.1)	-0.2 (0.1)	0.4 (0.5)	- -
Fall 1979	-0.1 (1.0)	0.0 (1.1)	0.0 (0.5)	- -
$45^{\circ}N-55^{\circ}N$				
Spring 1979	0.1 (1.2)	-0.2 (0.3)	- -	-0.1 (0.3)
Summer 1979	-0.8 (1.4)	-1.9 (0.9)	-0.7 (0.3)	-1.0 (0.2)

data were dropped from the NMC operational analysis north of $30^{\circ}N$, thus pairs are not available for fall in this band.

In summary, it appears that the satellite/ship product, averaged in zonal bands around the globe, improved between spring and fall, 1979 in the tropics relative to in situ measurements. Much of this apparent improvement resulted from algorithm changes which now require additional independent testing. Additional tests must also determine if the zonal averaging allows large differences of opposite sign in the same band to cancel each other (see below). At higher latitudes the time trend of the differences is substantial. In addition, the differences are large enough (Table 2) to raise serious doubts as to the usefulness of the satellite data in developing an operational SST product at mid to high latitude. It is not known if the difference at these latitudes has a seasonal component, or is due to instrumental drift or to algorithm difficulties.

4.2 Spatial Comparison

Monthly summaries of radioed ship SST (T_{SHIP}) on a 2° grid in both oceans were subtracted from T_{NMC}, normalized by σ_{FNOC} and projected on to a 5° grid. The resulting differences are directly comparable with those of Section 2.2 (Fig. 2) and demonstrate the effect of satellite SST on the blended NMC product. Typical results for July 1979 and January 1980 are shown in Figure 3.

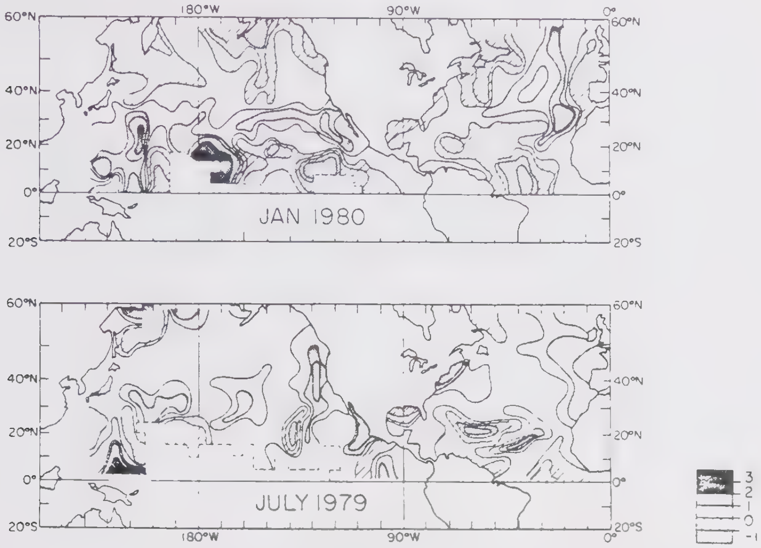

Fig. 3: The SST difference fields obtained by subtracting in situ measurements from the National Meteorological Center SST product (i.e. NMC-Ship). The differences are again normalized by the standard deviation from the FNOC data fields making them directly comparable with Figure 2.

The largest differences in Figure 3 occur south of 30°N where both satellite and ship data contribute to T_{NMC}. Values of one or more standard deviations are common. The differences are generally positive and always demonstrate high spatial coherence. The differences in this region are consistently larger than those associated with ship-only SST products (Fig. 2). The changes in satellite algorithm noted above are not apparent but then the limited ship data does not allow a comparison over the whole tropical region.

In latitudes above 30°N the differences are largest in the regions of high SST gradient (off the east coasts of the continents and in the northern-most regions of the oceans. Note the large bias (0.5 - 1.0σ) over the midlatitude ocean in July. The problem largely, but not completely, disappeared in October when the satellite data was deleted from the analysis.

The largest differences in both oceans are again rather regional in nature. For instance, in the data rich areas off the coasts of California, Mexico and Central America, $T_{NMC} > T_{SHIP}$ by 1-2°C in nearly all months irrespective of algorithm changes, etc. Much the same situation occurs off the west coast of North Africa and in the western equatorial Pacific. We can only conjecture as to the reasons for these regional variations. It is clear, however, that zonal or global averaging will seriously distort these characteristics of the difference fields.

In summary, the blended satellite/ship SST fields are in many respects similar to the ship/ship differences north of 30°N after October 1979. Prior to that time there is a substantial bias between the two fields that is apparently due to the satellite SST's. Besides this bias, the major differences are regional in nature, e.g., along the eastern margins of the oceans. Below 30°N the differences are 1σ or more, spatially coherent and have long time scales. They again have a regional character. It may be concluded that zonal averaging, as we did in the previous section, may give an overly optimistic estimate of the comparability of SST products. Such gross averaging should be avoided in further intercomparison work.

5. CONCLUSIONS

A limited intercomparison of supposedly similar maps of monthly mean SST for the North Pacific and Atlantic Oceans lead to the following conclusions:

a) Differences between SST products derived from in situ data alone exceed one standard deviation in areas of high SST gradient and/or low data density. These differences seem due to the editing/averaging/smoothing methods used on the reported data plus the inclusion of climatology in some products and not others. In any event, the difference field can have large time and space scales reminiscent of naturally occuring SST anomalies.

b) Differences between satellite influenced SST products and those derived solely from in situ data are spatially similar to, but numerically larger than noted above. The deletion of satellite data north of 30°N reduces the difference field to levels comparable to those obtained from ship/ship intercomparisons alone. South of 30°N the satellite influenced products seem to be biased over much of the ocean, particularly near the eastern margins and in the western equatorial Pacific.

c) The highly regional nature of the differences between SST fields makes it unwise to express their dissimilarities in terms of zonal and/or global averages. Such characterization may lead to an overly optimistic view of their correspondence.

d) The differences between SST fields produced with or without satellite data can be so large as to preclude the interchangeable use and/or blending of any two fields without serious risk of erroneous conclusion.

e) The time is ripe for those who construct SST products to collectively agree on a common method of analysis.

6. ACKNOWLEDGEMENTS

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SIMPLE, CONTINUOUS-FLOW SYSTEMS FOR DISSOLVING THE WATER-SOLUBLE COMPONENTS OF CRUDE OIL INTO SEA-WATER FOR ACUTE OR CHRONIC EXPOSURE OF MARINE ORGANISMS*

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Abstract—A continuous flow apparatus, referred to as a solubilizer, was constructed to dissolve the water-soluble fraction (WSF) of crude oil into water for short and long-term experiments with marine organisms. The basic solubilizer system consists of an oil reservoir, oil pump, modified glass bottle, and oil waste reservoir. This system dissolves the water-soluble components of crude oil without the loss of the more volatile compounds and without the formation of emulsions or oil droplets. Four solubilizer systems (two continuous flow and two recirculating) were evaluated for their efficiency in extracting the water-soluble components from Cook Inlet crude oil by analyzing for six monoaromatics over a 96-h period of continuous operation. When a solubilizer system was started, a stable concentration of the monocyclic aromatics in the water-soluble fraction was reached within 24 h. The water quality of the WSF effluent was not altered markedly in the continuous (open) flow systems, but there was a substantial reduction in dissolved oxygen in the recirculated (closed) systems. A single solubilizer system (open flow) with a 3 ml min^{-1} oil flow and a 1 l min^{-1} sea-water flow generated approx. 1.4 ppm of the total monoaromatics, which includes benzene, toluene, ethylbenzene and the three xylene isomers. This concentration varied depending on physical parameters and the chemical composition of the crude oil and water. With only slight modifications of the basic continuous flow system, a higher concentration (>3.4 ppm total monoaromatics) of the water-soluble fraction of crude oil was achieved. By recirculating the water supply, concentrations of 6.7–11 ppm total monoaromatics in the WSF were produced. The stability, reproducibility, and reliability of the four systems were demonstrated in several experiments. Researchers working in aquatic systems with crude oil can well appreciate a simple system that is easily cleaned, relatively maintenance-free, and which produces stable, reproducible concentrations of the WSF over extended periods of time. The increasing demands for ecological studies on aquatic organisms with crude oil, a difficult mixture of chemicals with which to work, precipitated the development of these solubilizer systems.

INTRODUCTION

The need to investigate the effects of hydrophobic chemicals on aquatic organisms and to maintain a specific concentration of these chemicals in water over an extended period of time has posed many problems, especially when the chemicals are soluble at less than 1% in water (e.g. crude oil, Bunker C, organophosphates, chlorinated hydrocarbons, phthalates and PCBs, see Gunther *et al.*, 1968). Each category of chemicals has inherent properties which require a unique method for dissolving and maintaining a specific concentration of that chemical in water. Consequently, several methods and modifications of these methods have been used to produce solutions of relatively insoluble chemicals in water (Mount & Brungs, 1967; La Roche *et al.*, 1970; Taras *et al.*, 1971; Brungs, 1973; Benoit & Puglisi, 1973; Lichatowich *et al.*, 1973; Benville & Korn, 1974; Bean & Blaylock, 1977; Vanderhorst *et al.*, 1977a; Hyland *et al.*, 1977; Roubal *et al.*, 1977).

Crude oil is a complex mixture of many chemicals varying in solubility from 0.004 ppm or less to 1933 ppm or more (Klevens, 1950; Gerarde, 1960; Peake & Hodgson, 1967; McAuliffe, 1969; Anderson *et al.*, 1974; Benville & Korn, 1977). In addition to differences in solubility of the various components, there are many other physical and chemical variations and interactions within a multicomponent system which make it difficult to produce and maintain a consistent concentration of the oil components in water (Leinonen & MacKay, 1973; Vanderhorst *et al.*, 1977b; Craddock, 1977). After considering a number of existing designs for solubilizing relatively insoluble compounds, we tried a semiclosed system that had been used successfully by Krugel *et al.* (1978) to solubilize components of jet fuel into water. This apparatus was duplicated at our laboratory in an attempt to dissolve the water-soluble components of crude oil. We found, however, that we could not use an adequate sea-water flow (1 l min^{-1}) without creating

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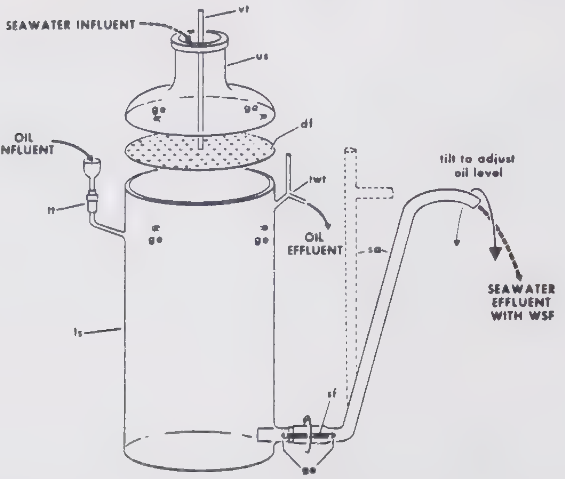

Fig. 1. Solubilizer: A modified 9.5-l. Pyrex bottle for extracting petroleum hydrocarbons from crude oil into sea-water; us—upper section (130 mm); vt— vent tube (6 mm O.D. × 152 mm); ge—glass ear; df—diffuser plate (20 gauge × 178 mm dia.) with fifty-four 1.6 mm holes; ls—lower section (345 mm); tt—thistle tube (10 mm O.D. × 160 mm) with a 12/30 glass joint and a 120° bend; twt—three way tube (10 mm O.D. with three 30 mm extensions); sa—side arm (20 mm O.D.) with a 24/40 glass joint; sf—spring fastener (70 mm).

numerous oil droplets in the sea-water effluent; moreover, the system was incapable of maintaining a stable concentration of the water-soluble fraction (WSF) without continually replacing the crude oil. This paper describes flow-through solubilizer systems which will provide researchers with a simple, inexpensive dosing apparatus for aquatic toxicological studies with crude oil.

MATERIALS AND METHODS

Basic solubilizer components

The basic system for dissolving the WSF from crude oil consists of an oil reservoir (19 l. Corning* Pyrex solution bottle) with a 4 mm Corning Teflon stopcock; a fluid metering pump with scavenger slot (Model RPIG 50/csc, Fluid Metering, Inc., 48 Summit St, Oyster Bay, NY 11771, U.S.A.); Tygon tubing special formulation F4040; and a solubilizer bottle (9.5 l. Corning Pyrex solution bottle) modified as described below by General Glassblowing Co., 1107 Ohio Ave, Richmond, CA 94804, U.S.A.

Solubilizer bottle

The 9.5 l. bottle (Fig. 1) was cut horizontally 130 mm from the top and the two cut edges ground. The two portions referred to as the upper (smaller) and the lower (larger) sections are held together by 3–50 mm spring fasteners. Six glass hooks (glass ears) for the spring fasteners were heat-sealed onto the glass bottle at three equidistant points around the bottle, 25 mm above and 50 mm below the cut.

For the upper section, a circular diffusion plate (178 mm dia.), was cut from a 20-gauge stainless-steel sheet. A 6.2 mm hole was drilled in the center of the plate for a vent tube and fifty-four 1.6 mm holes were drilled in a concentric pattern at 19 mm intervals around the diffusion plate. The glass vent tube (6 mm o.d. × 152 mm) was inserted 6 mm into the diffusion plate and affixed in place with silicone sealant. The diffusion plate was inserted 6 mm into the upper section of the bottle with the vent tube extending out of the top of the upper section and the plate affixed in place with silicone sealant.

In fabricating the lower section, three glass tubes were sealed into the bottle to provide an influent and effluent for the oil and an effluent for the sea-water containing the dissolved WSF.

The oil influent tube was a 10 mm o.d. × 160 mm glass thistle tube with a standard taper 12/30 ground glass joint located 60 mm from the top of the thistle tube. A bend of 120° was made in the lower end of the tube 30 mm from the end, and the end of the tube sealed into the glass bottle 76 mm below the horizontal cut of the bottle.

An oil effluent tube (10 mm o.d. × three–30 mm extensions) was sealed into the opposite side of the bottle from the oil influent tube. The three-way tube was attached 38 mm below the cut of the bottle.

The sea-water effluent tube (20 mm o.d. × 50 mm) with a 24/40 glass joint (inner part) was ring-sealed 30 mm above the bottom and 25 mm into the bottle. An S-shaped side arm was formed from a 20 mm o.d. × 430 mm tube with a 24/40 glass joint (outer part). The vertical height between the bottom of the bottle and the overflow point of the S-shaped tube was 300 mm. A glass side arm with 90° bends, as illustrated in Fig. 1 by the dotted lines, also has been used successfully and is superior from a space viewpoint. The side arm was secured to the bottle by 2–70 mm spring fasteners between 4 glass ears. Two glass ears were sealed onto each glass joint at a distance of 60 mm from the end of the joint.

Solubilizer operation

A continuous flow single solubilizing apparatus was set up as shown in Fig. 2. Six liters of sea-water were poured into the 9.5 l. solubilizer bottle followed by 1.5 l. of Cook Inlet crude oil, which resulted in a 38 mm band of oil on

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* Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

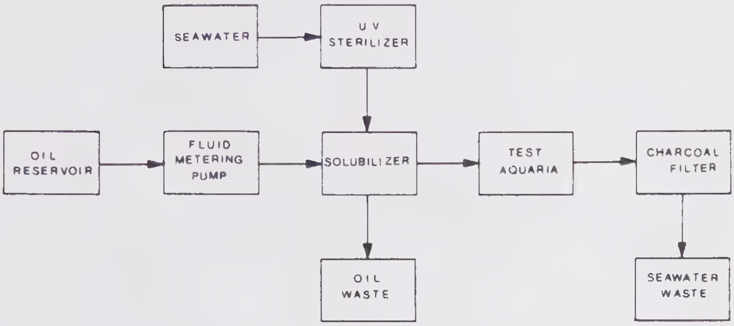

Fig. 2. An open flow dosing system that sterilizes the sea-water and removes the WSF from the effluent.

top of the sea-water. Silicone grease was applied to the horizontal joint of the upper and lower sections of the bottle. The top was put in place and secured by three–30 mm spring fasteners. The metering pump was turned on with the pump adjusted at 2 to provide a 3 ml min^{-1} flow of crude oil through the bottle. A 1 l min^{-1} flow of sea-water was introduced at the top of the bottle. The side arm was rotated laterally until its height was 18 mm lower than the top of the oil layer. This 18 mm difference maintained a layer of oil 38 mm deep within the solubilizer. If the side arm was lowered or raised from the above setting, the volume of oil in the bottle increased or decreased respectively. The exact position of the side arm depended on the specific gravity of the crude oil and the salinity of the sea-water.

Sea-water entering the top of the bottle was dispersed into small droplets as it passed through the diffuser plate. Each droplet of sea-water passing through the oil layer dissolved some of the water-soluble portion from the crude oil. Within 24 h, a stable concentration of the WSF in the sea-water effluent was obtained and the system was ready for exposing organisms.

In an effort to reduce possible contamination and losses of the WSF, the lower part of the solubilizer should be of all-glass construction. In addition, all-glass delivery lines were used between the solubilizer and aquarium, with the glass tube extending to the bottom of the test aquaria. All water entering the system was sterilized with a flow-through germicidal ultraviolet light system (Model RM-2-15, Refco, P.O. Box 2356, San Leandro, CA 94577, U.S.A.).

The expense of the basic continuous flow system is approx. $500–600, with the liquid metering pump comprising about one-half ($310) the total cost of the system. A modified 9.5 l. (2.8 gal) solubilizer bottle with the diffuser plate cost $90. An additional expense is required for the cascading and recirculating systems described below because of the extra components, i.e. solubilizer bottles, water pump, modified aquarium, and water bath. The u.v. disinfection unit is also an added expense.

Solubilizer modifications

Two modifications of the basic system were used in order to increase the concentration of the WSF: (1) a cascading system with three solubilizers connected in series; and (2) a recirculating system using one solubilizer unit and a recirculating pump. In the cascading system (Fig. 3), each solubilizer is elevated 200 mm above each succeeding solubilizer in series. The WSF leaving the first solubilizer flows by gravity into the second and the sea-water effluent of the second flows into the third solubilizer. Also, the crude oil entering the first solubilizer flows by gravity through the other two solubilizers.

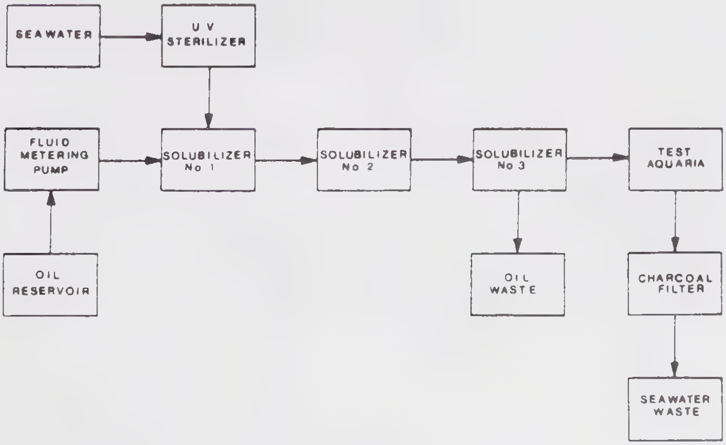

Fig. 3. An open flow dosing system used to increase the WSF concentration by adding solubilizers in series.

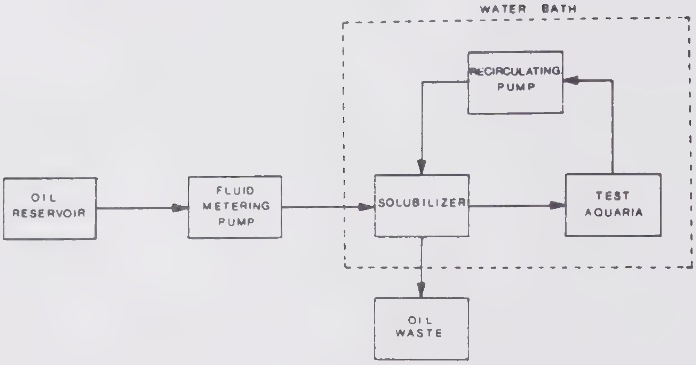

Fig. 4. A semi-closed system used to increase the WSF concentration by recirculating the sea-water and continually replacing the crude oil.

Two recirculating systems were constructed (Fig. 4): a small system excluding the test aquaria with a 6-l. capacity to obtain a high concentration of the WSF and a larger system including the test aquaria with a 36-l. capacity for use with aquatic organisms. In both recirculating systems the oil flowed through the solubilizer at 3 ml min^{-1}, and the sea-water was recirculated by a submersible March pump (Model 1A-MD-1), using a Hoffman clamp to restrict the water flow to 1 l min^{-1}. A 114-l. (30-gal) aquarium was used as a water bath to maintain a constant water temperature in the 6-l. system and two 114-l. aquaria for the 36-l. system.

Effluent analysis

Water samples (100 and 1000-ml volumes) with 4-ml of 6 N HCl added were extracted with 10-ml of TF Freon (trichlorotrifluoroethane) to remove and concentrate the six monocyclic aromatics (benzene, toluene, ethylbenzene, *p*-xylene, *m*-xylene and *o*-xylene) from the sea-water. The 100 and 1000-ml samples were extracted once and 3 times with TF Freon, respectively. Separation and quantitation of the aromatics were accomplished using a Micro-Tek 220 gas chromatograph with a dual flame ionization detector, a 1.8-m (6-ft) column containing 5% Bentone 34/5% SP 1200 on 100/120 mesh Supelcoport and another 1.8-m (6-ft) column containing 5% Bentone 34/5% didecylphthalate on 80/100 mesh chromosorb PAW. The column packings were obtained from Supelco, Inc., Bellefonte, PA 16823, U.S.A. Concentrations were determined using a Hewlett–Packard 3380A integrator.

RESULTS

Data obtained over a 4-day period from the continuous flow (single and multiple solubilizer) systems and a recirculation system are summarized in Table 1. Water samples taken 3 times daily were analyzed, data averaged and the standard deviation computed. The data indicate that the best long-term stability is achieved with a single solubilizer system, and that the variation in the concentrations of the monoaromatics increases in the multiple and recirculation systems, respectively. Benzene was highest in concentration followed by toluene, *m*-xylene, *o*-xylene, ethylbenzene and *p*-xylene. *Para*-xylene could not be detected in the WSF from a single solubilizer system because its concentration was below the lower limit of our analytical technique. The limit of detectability of our analytical method ranged from 0.001 to 0.10 ppm depending on the aromatic analyzed. By using additional solubilizing units in series (multiple system), the concentration of each aromatic was increased over the single solubilizing system. Recirculating 36 l. of sea-water continuously through the crude oil increased the concentration of most of the monoaromatics over the single and multiple systems. In regard to total monoaroma-

Table 1. Mean concentrations of six monocyclic aromatics in the sea-water effluent from three solubilizer systems

Components	Single*		Multiple		Recirculating		Limit of detectability
	Concentration (ppm)	Benzene ratio	Concentration (ppm)	Benzene ratio	Concentration (ppm)	Benzene ratio	
Benzene	0.62 ± 0.079	1.000	1.6 ± 0.21	1.000	3.9 ± 0.86	1.000	0.10
Toluene	0.53 ± 0.044	0.869	1.3 ± 0.12	0.843	2.2 ± 0.45	0.572	0.025
Ethylbenzene	0.045 ± 0.023	0.070	0.080 ± 0.020	0.055	0.080 ± 0.05	0.021	0.021
p-Xylene	ND† ± —	—	ND† ± —	—	0.010 ± 0.01	0.003	0.001
m-Xylene	0.052 ± 0.0085	0.085	0.16 ± 0.050	0.104	0.28 ± 0.08	0.071	0.042
o-Xylene	0.032 ± 0.019	0.049	0.14 ± 0.020	0.087	0.22 ± 0.05	0.057	0.012
Total	1.2 ± 0.14	—	3.3 ± 0.36	—	6.7 ± 1.4	—	

* Experimental parameters: temperature, 14°C; salinity 30‰; dissolved oxygen, 8–9 ppm; oil flow, 3 ml min^{-1}; and sea-water flow, 1 l min^{-1}.

† ND = Not detected below 0.001 ppm for *p*-Xylene.

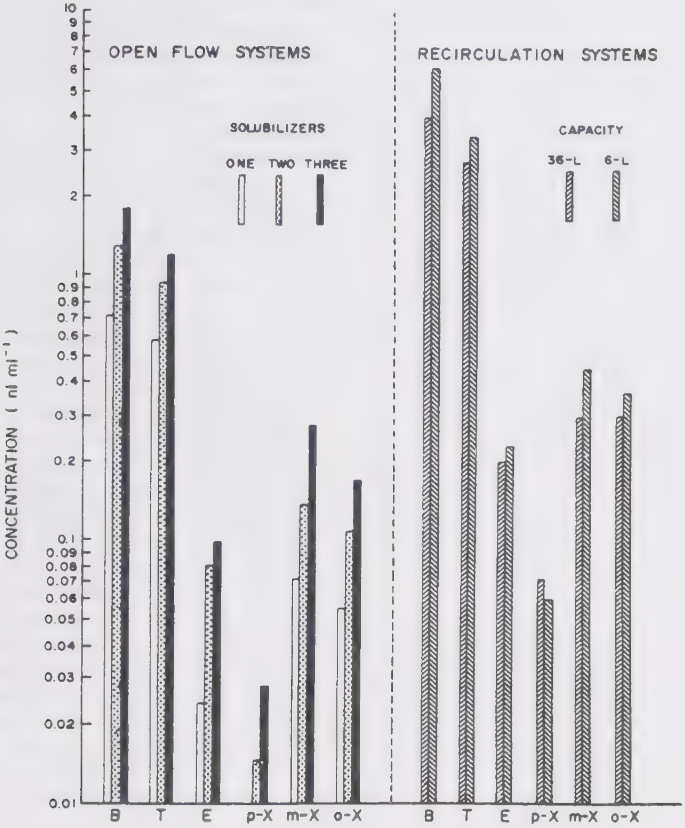

Fig. 5. Composition of six aromatics in the water-soluble fraction from different systems (B = benzene, T = toluene, E = ethylbenzene, *p*-X = *para*-xylene, *m*-X = *meta*-xylene and *o*-X = *ortho*-xylene).

tic data, the multiple system composed of three solubilizing units in series produced a monoaromatic concentration 2.8 times higher than did the single system, and the recirculation system yielded monoaromatic concentration 2.0 and 5.6 times higher than did the multiple and single systems, respectively. The aromatic ratios varied between each system as noted by the benzene ratios with the highest variation occurring in the recirculating system.

The bar graph in Fig. 5 illustrates the differences between and within open flow and recirculation systems. By using additional solubilizing units in series the concentration of each aromatic was increased. For example, the concentrations were nearly doubled, using two solubilizing units as opposed to a single unit. Adding a third unit further increased the concentration of the WSF in the sea-water effluent, but to a lesser extent than the dual unit system. Both recirculation systems generated a higher concentration of the WSF than the open flow system. However, the smaller recirculation system (6 l.) had a higher concentration of aromatics than the larger system (36 l.) except for *p*-xylene.

The most noted difference in water quality was observed in the reduction of the dissolved oxygen (DO) levels within the recirculation systems. In the two recirculation systems the average DO decreased from 9.3 to 5.4 ppm in the 36-l. system and 8.1–3.4 in the 6-l. system. The DO level was proportional to the volume of sea-water used in the recirculation system. There was only a slight drop in the DO content of the sea-water as the water passed through each solubilizer in the open system (0.3–0.4 ppm reduction for each solubilizer). The temperature of the recirculation systems was controlled by placing the solubilizer system into a water bath. A slight increase was noted in the temperature (+0.2°C) of the sea-water as it passed through each solubilizer in the open flow system. The salinity of the sea-water was not affected in any of the systems.

DISCUSSION AND CONCLUSION

Four solubilizer systems were constructed and tested which extract the WSF from crude oil and maintain a stable concentration of the WSF over an extended time period without the formation of oil droplets or emulsions. The described solubilizer systems operate on the principle that the liquid being extracted floats on water and is relatively immiscible in it. Cook Inlet crude oil, which is an "insoluble" liquid with a low specific gravity, meets these criteria. The crude oils obtained from various wells in the Cook Inlet area range in specific gravity from 0.764 to 0.899 (Blasko *et al.*, 1972).

The described solubilizer systems were designed for a sea-water flow of 1 l min^{-1} through a 38-mm oil layer with an oil flow of 3 ml min^{-1}. Variations in the operating parameters of the solubilizer, as well as the chemical composition of the crude oil itself, will affect the composition and concentration of the WSF leaving the solubilizer, e.g. sea-water and oil flow rates, oil layer depth, salinity and temperature. The operating parameters of importance to our research were the flow rates of the sea-water and the oil, and the variation in the depth of the oil in the solubilizer. Salinity, temperature and crude oil compositions were factors that were held constant in our experiments to determine the sublethal effects of Cook Inlet crude oil on the aquatic food chain.

We will consider first the effect of changing the sea-water flow rates above and below 1 l min^{-1}. Reducing the sea-water flow rates below 1 l min^{-1} altered the composition of the WSF leaving the solubilizer and reduced the efficiency of the solubilizer system, since the sea-water entering the solubilizer will flow through fewer holes in the diffuser plate. A sea-water flow rate greater than 1 l min^{-1} will reduce the concentration of the WSF in the sea-water. At flow rates above 1.6 l min^{-1}, oil droplets will begin to form since the vertical velocity of the sea-water flowing through the bottle exceeds the buoyancy of the oil droplets. Use of other liquids with a higher specific gravity than Cook Inlet crude oil may require reduction of the sea-water flow rate or construction of a solubilizer bottle with a larger diameter to reduce the velocity of the seawater moving through the upper liquid layer, in order to avoid the liquid droplet formation. If higher water flows are needed, the latter alternative mentioned would be the most appropriate method. Conversely, the sea-water flow rate could be increased, using a crude oil or other immiscible liquid with a lower specific gravity than Cook Inlet crude.

Also, oil droplets can be expelled from the solubilizer when emulsions are formed. Sharpley (1966) has stated that certain microorganisms interacting with crude oil will produce surfactants, in addition to the surfactants already in the crude oil that will increase the oil emulsion problems. We have observed oil emulsions forming after 2 weeks of continuous operation of a solubilizer system. In an effort to reduce the bacteria entering the solubilizer, an ultraviolet (u.v.) sterilizer was used to treat the sea-water influent. The u.v. dose suggested by most manufacturers is 33,000 microwatt seconds per square centimeter (μWs cm^{-2}) for destruction of pathogenic organisms. However, higher doses are needed to destroy other microorganisms, especially spores (Nagy, 1964). We are currently experimenting with u.v. doses above 70,000 μWs cm^{-2}.

An increase in the oil flow rate will increase the concentration and alter the composition of the WSF. However, as a matter of practical logistics we chose 3 ml min^{-1}, which consumes over half of a barrel of crude oil per month for one continuously-operating solubilizer system. The depth of the layer of oil in the solubilizer was arbitrarily chosen. We noticed a reduction in the concentration of the monoaromatics in the WSF when the oil layer was reduced below 22 mm in depth. Increasing the depth of the oil layer beyond 22 mm did not appreciably change the concentration of the monocyclics.

The 19 mm distance between holes in the diffusion plate was adequate to keep the individual water droplets from coalescing before they came into contact with the oil layer. The 1.6 mm holes were the optimum size since larger holes allowed larger water droplets, which did not dissolve as much of the WSF from the crude oil and smaller holes tend to clog.

In an effort to reduce the WSF losses via sorption after the WSF leaves the solubilizer, all delivery tubes and aquaria should be made of glass. Volatilization losses can be reduced by expelling the WSF into the bottom of the aquarium and placing a glass cover over the aquarium when possible. The glass cover eliminates the moving air currents, which reduces the partitioning action of the volatile organics with the air.

The National Marine Fisheries Laboratory in Auke Bay, Alaska evaluated a similar single solubilizer system, as illustrated in Fig. 2, and found it to be very stable over a 6-day interval. They maintained the same experimental conditions as we did except for the lower temperature of 4°C. Their values for the total monoaromatics were slightly higher than ours (1.8 ppm), but the relative proportions of monoaromatics were the same. They also analyzed for some diaromatics and found the following average concentrations: naphthalene, 36 ppb; 2-methylnaphthalene, 19–21 ppb; dimethylnaphthalene, 11–12 ppb; and total diaromatics, 67–68 ppb. Our values for the diaromatics were 14–30% lower*. The lower values in the amounts of aromatics would be attributable to the difference in water quality of the two laboratories (e.g. minerals, organics, temperature, etc.).

We have tried the solubilizer system using a single component, benzene, which is one of the main components in most crude oils. A 1 l min^{-1} sea-water flow through a 38 mm layer of benzene produced a 200 ppm benzene concentration in the sea-water effluent leaving the solubilizer. As a matter of interest, a 38 mm layer of Cook Inlet crude oil resulted in a 0.72 ppm benzene concentration at equilibrium, which is a much lower concentration when the benzene is extracted from a multicomponent system. Leinonen & MacKay (1973) have gone into great detail in explaining the characteristics of single and multicomponent systems.

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* Sid Korn, unpublished data, cited with permission.

We have reused Cook Inlet crude oil in other experiments and have found the ratio of the monoaromatic components did not change appreciably, although there was a slight decrease in concentration. The ability to reuse the crude oil makes multiple solubilizer systems more practical if oil supplies are limited.

In summary, this paper describes a method to dissolve the water-soluble components from a crude oil into sea-water. The concentrations of the monoaromatics measured from several experiments over many days of operation have demonstrated the stability, reproducibility and reliability of the system that lends itself to recirculating and continuous flow studies for extended periods of exposure. The system is relatively inexpensive and requires minimal space and maintenance. A wide range of desired concentrations of the WSF of crude oil can be achieved with only slight modifications of the basic design, as illustrated in the figures. Researchers using the recirculating systems with aquatic organisms should be aware of increasing metabolites and decreasing DO levels, as in any static system. The 1 g biomass per 1 l. water guideline should not be exceeded. Additional experiments using fish, invertebrates and phytoplankton (Nunes & Benville, 1978, 1979a, b) illustrate the stability of the system and the effectiveness of this method in investigating the biological impact of oil*.

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* Detailed information on the mean concentrations found in Table 1 and other concentration data from other experiments may be obtained from the senior author.

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Burnt Tuna: Conditions Leading to Rapid Deterioration in the Quality of Raw Tuna

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ABSTRACT—Burnt tuna is raw tuna which is paler and softer than normal. This study indicates that the burnt tuna condition results from muscle cell degeneration which begins prior to the death of the fish and proceeds more rapidly after death than in normal tuna. Female sex, longer fighting times, and less efficient chilling are positively correlated with the occurrence and severity of the burnt tuna condition.

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Introduction

In Hawaii, raw tuna flesh which seems paler and softer than normal is characterized by buyers as being "burnt." High-quality tuna should be translucent, red, and firm. Burnt tuna, because of its poor texture, color, and slightly sour taste, while edible, is undesirable for raw consumption (as "sashimi"). It therefore commands only a fraction of the selling price of high quality tuna, depending on the extent and the severity of burn. However, the burnt condition is not absolute in extent or degree; the affected area can vary from 5 to 100 percent of the total marketable meat of the fish and range in severity from marginal to severely burnt. The variability in occurrence compounds an already difficult diagnostic problem.

The condition periodically occurs in the large (45-136 kg) tropical tunas—the yellowfin tuna, *Thunnus albacares,* and bigeye tuna, *T. obesus*—and was first brought to the attention of the National Marine Fisheries Service (NMFS) in 1974 by recreational fishermen who troll off Hawaii's Kona coast. The problem is now a major economic concern of the night handline fishery of the same island. This highly effective, cost efficient industry, found only in Hawaii and in the Philippines (Yuen, 1979), would be an excellent candidate for fishery development in export-poor Pacific island nations if the burn problem could be controlled. Whatever the causes of burn, we suspect that the problem is exacerbated by the limited chilling facilities found aboard most night handline and recreational fishing boats.

In Hawaii, traditional marketing practices delay the discovery of burn. A typical fish changes hands at least twice in the first 48 hours after death. The fisherman consigns his catch to a wholesaler who then either sells it locally or ships it to a more distant market. If the fish is sold locally, the fish is butchered and the burn is discovered relatively quickly, within 12 hours of catching. However, if it is exported, butchering usually occurs after the fish is sold to the last and most distant retailer, from 36 to 60 hours after catching. Transportation costs have thus been incurred before discovery of the condition.

Upon discovery of burn, the fisherman is required to refund a portion of the auction price to the wholesalers which is then used to defray a fraction of the costs involved in the marketing and shipping. Rebates on burnt fish were reported to range from 5 to 75 percent of the original selling price in 1977. Annual losses to the night handline fishermen were estimated to be about 16 percent of the total value of the catch (Cramer et al.)[1].

Clearly the reduction of burn through improved fishing and handling methods is an important goal and some method must be developed to identify the condition of the fish early in the marketing sequence before filleting.

These requirements formed the motivation for our work. We reasoned that our best strategy to investigate burn was to correlate quality of the fish with those measurable variables that would be likely to be responsible for, or at least indicate burn. Those correlates fell into three classes: 1) Fishing variables such as time of the year, temperature of the water, fighting time, and care of the catch; 2) biological characteristics such as sex, weight, species, and body temperature at death and after; and 3) biochemical, histological, and pH samples. We hoped that burnt fish would exhibit some differences in key characters relating to exercise or flesh quality. Thus, differences between burnt and normal tuna would indicate the causes and suggest remedies.

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Materials and Methods

Fish

Bigeye and yellowfin tunas were studied in this report. Three tunas were obtained from commercial fishermen on the island of Hawaii. Seven fish were caught off Kona, Hawaii, and transported live in the baitwell to the Kewalo Research Facility (KRF) in Honolulu and two fish were held in captivity at KRF for over 6 months before being used in these studies.

The date, area of catch, fighting time, weight, species, and sex of the fish were recorded. The prechill interval (the time from landing to chilling) was also recorded.

Sampling and Testing

Temperature, blood, and muscle samples were recorded when the fish were: 1) First landed on the boat, 2) off-loaded from the boats, and 3) at 24 hours after off-loading.

Blood was obtained by cardiac puncture immediately after boating the fish using silicone-coated vacutainers (Kimble-Terumo, Elkton, MD.).[2] Captive fish were bled just prior to killing, and 2 ml of whole blood were immediately mixed with 2 ml of 15 percent perchloric acid for glucose and lactate determinations. The serum was separated from the remaining blood and frozen for later testing.

A coring tool was used to obtain tissue samples from the deep muscle near the vertebral column. Tissues were frozen on dry ice or fixed in Dietrich's solution. The latter tissues were processed to obtain Hemotoxylin and Eosin stained sections for microscopic examination.

An electronic thermometer with a 12 cm probe was used to obtain temperatures of deep (11 cm) or superficial (just under the skin) tissues of fish.

Fish held in captivity or transported live to KRF were placed in ice water for 4-8 hours after killing to simulate normal commercial procedures for treatment of fish prior to off-loading.

The handling of fish during the first 24 hours after off-loading from the boats was evaluated and categorized. The fish were designated to have received: 1) Excellent treatment when stored in ice water at 0°C, 2) fair treatment when stored in refrigerators at 5°C, and 3) poor treatment when stored at ambient temperature of 28°C.

After the fish were auctioned and quartered, the flesh was graded and scored on the basis of color and texture as: Excellent, 1 point; good, 2 points; marginal, 3 points; poor, 4 points; and very poor, 5 points. These subjective evaluations were corroborated by discussions with the auctioneer and correlated with the price received per pound of fish.

Tests

Blood lactate and glucose concentrations were determined by enzymatic analysis utilizing the conversion of NAD to NADH as described by Burgmeyer (1974). A creatine phosphokinase (CPK) assay was also conducted following the method of Burgmeyer (1974). The above assays were performed at the University of British Columbia, Vancouver, with the direction and assistance of P. Hochachka and J. Balantyne.

The pH of muscle tissue was determined by titration and the amount of potassium carbonate required to lower the pH of the muscle suspension to a pH of 5.6-6.0. A pH meter with a 4 mm diameter probe was used to determine the pH of the midsection and tail muscle tissue of yellowfin or bigeye tuna on the auction floor. The pH was also determined by pH meter for macerated muscle tissue suspended in distilled water.

Statistical Analysis

Correlations of quantitative variables were determined by simple regression analysis. Correlations involving one or more nonparametric variables were determined by using Spearman's correlation rank test (Snedecor and Cochran, 1967).

The significance of differences between mean values were determined using a t test for the differences of means (Snedecor and Cochran, 1967).

Results

The fighting time and other relevant data on the 12 fish used in this study are recorded in Table 1. Significant ($P<0.05$) positive correlations were found between fighting time and concentrations of blood lactate (Fig. 1) and blood glucose (Fig. 2) at death and between fighting time and tissue lactate (Fig. 3) when fish were being off-loaded from the boats. A negative correlation was found between fighting time and relative acidity of muscle at off-loading (Table 2). The correlations of these parameters are also indicated in Table 2.

There was a significant difference ($P<0.05$) between sexes in quality of flesh of fish over 30 kg in weight (Table 3). The flesh of female fish was more often of low quality. An interaction was found between

Table 1.—Data on fish studied.

Date caught (1978)	Area caught	Fighting time (min.)	Wt. (kg)	Species	Sex
21 Aug.	Hilo[1]	9	115.8	*T. albacares*	M
21 Aug.	Hilo[1]	10	63.6	*T. albacares*	F
27 Sept.	Kewalo[2]	15	10.8	*T. albacares*	F
27 Sept.	Kona[2]	9	5.2	*T. obesus*	M
27 Sept.	Kona[3]	9	4.4	*T. obesus*	M
27 Sept.	Kona[3]	4	3.4	*T. albacares*	F
27 Sept.	Kona[3]	4	3.5	*T. albacares*	F
27 Sept.	Kona[3]	12	3.7	*T. albacares*	M
27 Sept.	Kona[3]	18	3.6	*T. albacares*	M
27 Sept.	Kona[3]	31	3.5	*T. albacares*	F
17 Oct.	Kewalo[2]	0	9.4	*T. albacares*	F
23 Oct.	Kona[1]	15	50.4	*T. obesus*	F

[1] Sampled at sea.
[2] Captive fish.
[3] Transported live to KRF.

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[2] Reference to trade names or commercial firms does not imply endorsement by the National Marine Fisheries Service, NOAA.

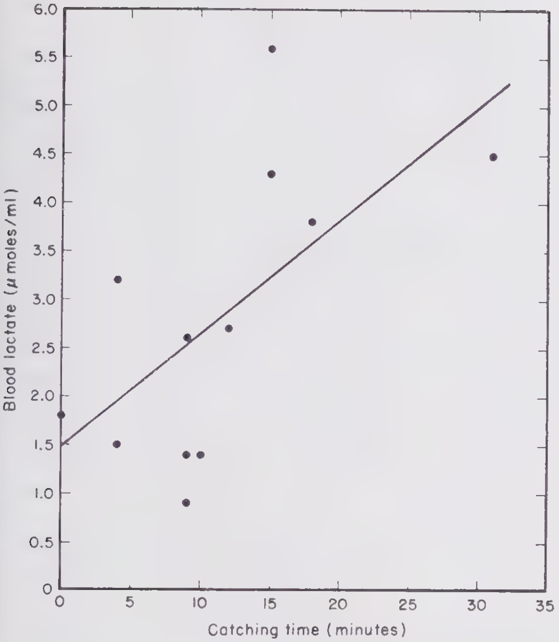

Figure 1.—Correlation between catching time (fighting time) and concentration of blood lactate at death. Line fitted by least squares methods.

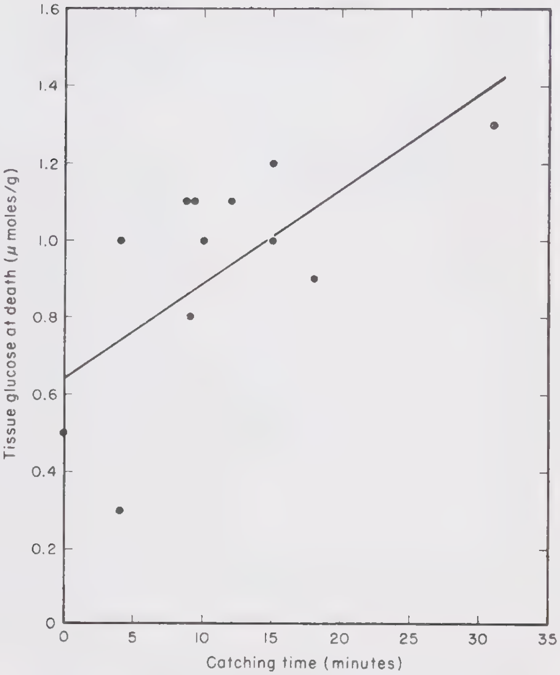

Figure 2.—Correlation between catching time (fighting time) and concentration of glucose at death. Line fitted by least squares methods.

Table 2.—Correlations between fighting time (FT), blood lactate level at death (BL), tissue glucose level at death (TGa), tissue lactate level at off-loading (TLb), relative acidity in tuna tissues at off-loading (TAb), and quality of fish at quartering (Q).

Independent variable	Dependent variable	Correlation
FT	BL	[1]0.64
FT	TGa	[1]0.69
FT	TLb	[1]0.59
FT	TAb	[1]-0.66
BL	Q	[2]0.82

[1] Significant at the 0.05 percent level.
[2] Significant at the 0.01 percent level.

Table 3.—The effect of size and sex on flesh temperature and flesh quality.

Body wt. (kg)	Sex	Temperature (°C)		Flesh quality[1]	
		Average	Range	Average	Variance
<11	M	27.5	26.9-28.4	2.4	1.3
<11	F	27.7	26-29.5	2.8	0.7
>30	M	29.6	29-31	1.5	1.0
>30	F	29.7	27-31	2.8	1.6

[1] 1 = Excellent, 2 = good, 3 = marginal, 4 = poor, and 5 = very poor.

Table 4.—Interactions between blood lactate levels at death and 24-hour treatments after off-loading.

Blood lactate micromole/ml	Quality at death[1]	Treatment[2]	Quality at quartering[1] (24 h after death)
0.91	1	Excellent	1
1.42	1	Excellent	1
1.42	1	Poor	3
1.47	1	Fair	2
1.82	2	Fair	2
2.58	2	Fair	2
2.67	1	Fair	2
3.20	2	Poor	3
2.83	1	Poor	4
4.25	3	Poor	4
4.49	2	Fair	3
5.64	2	Poor	4

[1] Quality was determined histologically and was scored as follows: 1 = Excellent, 2 = good, 3 = marginal, 4 = poor, and 5 = very poor.
[2] Excellent = stored in ice water at 0°C, fair = stored in refrigerators at 5°C, and poor = stored at ambient temperature of 28°C.

treatment after off-loading and concentrations of blood lactate at death (Table 4). Low lactate and good treatment resulted in excellent quality flesh; low lactate and poor treatment or high lactate and fair treatment resulted in marginal quality flesh; and high lactate and poor treatment produced poor quality flesh.

In some cases, there was excellent correlation between pH of muscle tissue and quality of tuna flesh (Table 5) while in other instances lower pH could not be correlated with poor quality flesh (Table 6, Fig. 4). These differences are probably due to differing temperatures and durations before auction (Nakamura et al., 1977).

No significant correlations were found between deep body temperatures and quality of fish or results of biochemical tests. Nor could signifi-

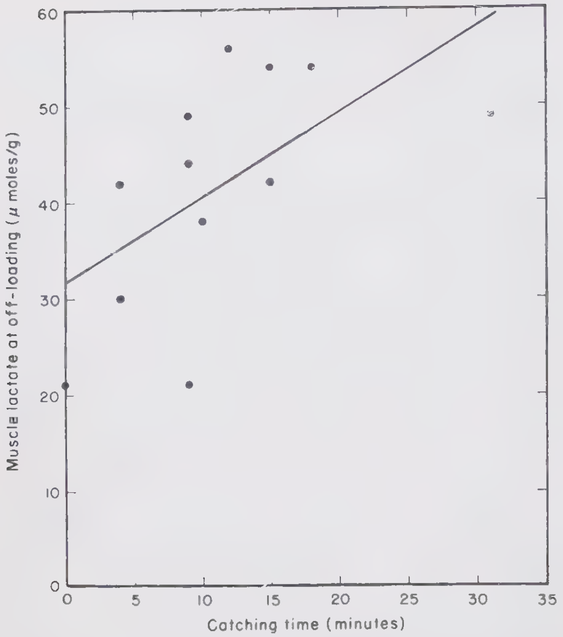

Figure 3.—Correlation between catching time (fighting time) and muscle lactate at off-loading. Line fitted by least squares methods.

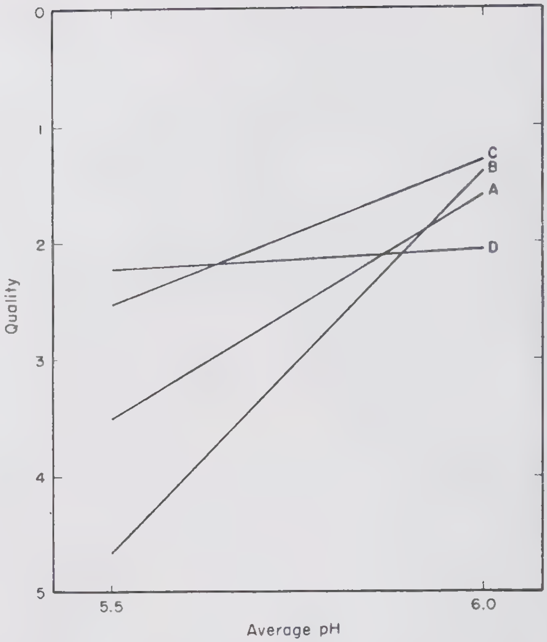

Figure 4.—Correlation between pH and auction quality (1 = excellent, 2 = good, 3 = marginal, 4 = poor, and 5 = very poor) of: A) all fish sampled, B) fish sampled on 28 July, C) Honolulu fish sampled on 10 August, and D) Hilo fish sampled on 10 August.

Table 5.—Quality and pH of midsections and tails of yellowfin tuna at the Honolulu fish auction, 28 July 1978.

	Tuna quality									
	Excellent		Good		Marginal		Poor		Very Poor	
	Mids	Tail	Mids	Tail	Mids	Tail	Mids	Tail	Mids	Tail
	6.0	6.1	6.0	6.2	5.6	5.7	5.6	5.6	5.4	5.5
	6.0	6.0	5.9	5.6	—	—	5.7	5.8	5.5	5.6
	6.0	5.7	5.9	5.9	—	—	5.8	5.9	5.7	5.8
	5.8	5.9	5.8	5.9	—	—	5.7	5.9	—	—
	6.0	5.6	—	—	—	—	5.6	5.7	—	—
	5.8	6.0	—	—	—	—	—	—	—	—
	5.9	6.0	—	—	—	—	—	—	—	—
Mean	5.93	5.90	5.90	5.90	—	—	5.68	5.78	5.53	5.63
Variance	0.01	0.03	0.01	0.06	—	—	0.01	0.02	0.03	0.03

cant correlations be found between the pre-chill interval and quality of fish or results of biochemical tests of blood and tissues.

Histopathologic studies of muscle from a limited number of fish revealed the following: 1) Inflammatory changes were not seen, suggesting that all changes occurred shortly before or immediately after death; 2) edema was seen in muscle obtained at the time of boating; 3) extensive edema and muscular degeneration were seen in burnt fish at the time of auctioning; and 4) tissue gram stain showed that bacteria was associated with the muscular degenerative changes.

Table 6.—Quality and pH of midsections and tails of yellowfin tuna at the Honolulu and Hilo fish auctions, 10 August 1978.

	Tuna quality					
	Excellent		Good		Poor	
	Mids	Tail	Mids	Tail	Mids	Tail
	Honolulu fish					
	5.6	5.6	5.5	5.6	6.0	5.5
	5.6	5.7	5.7	5.7	5.9	5.8
	5.9	5.9	5.6	5.7	—	—
	5.6	5.7	—	—	—	—
	5.7	5.8	—	—	—	—
Mean	5.68	5.74	5.60	5.67	5.95	5.65
Variance	0.2	0.01	0.01	0.00	0.08	0.02
	Hilo fish					
	5.8	5.9	5.8	5.8	5.7	5.8
	6.0	5.9	5.7	5.8	5.9	5.8
	—	—	5.9	5.9	—	—
	—	—	5.7	5.8	—	—
	—	—	5.9	5.9	—	—
	—	—	6.0	6.0	—	—
	—	—	5.8	5.8	—	—
	—	—	6.0	6.0	—	—
	—	—	6.0	6.1	—	—
	—	—	6.0	5.9	—	—
	—	—	6.1	6.1	—	—
	—	—	5.9	5.9	—	—
Mean	5.90	5.90	5.90	5.92	5.80	5.80
Variance	0.02	0.00	0.02	0.01	0.02	0.00

Discussion

As suspected by tuna fishermen, the results of this study suggest that the care and handling of fish after being caught is partly related to the subsequent quality of the flesh of the tuna (Table 4). However, the pathogenesis of burnt tuna may also be related to physiological changes in the fish during the struggle while being caught. Fighting time was related to blood lactate and glucose levels at death (Fig. 1, 2). The edema (abnormal accumulation of fluid) in muscle seen in histopathological studies of biopsies obtained at death also suggest that the struggle of fish being caught may predispose the flesh to subsequent degeneration. The lack of inflammatory changes at that time indicates that the condition is not developed prior to being hooked.

A hypothesis on the mechanism for the development of burnt tuna is as follows.

1) The struggle of fish while being caught may result in muscle edema, the severity depending on the intensity of the struggle. (Longer and more intensive struggling results in higher blood levels of glucose and lactate.)

2) The edema fluid of muscle presents a good medium for bacterial growth.

3) Chilling of fish after catching determines the temperature of the deeper portions of the fish muscles, which are least affected by external cooling procedures.

4) Poor chilling procedures allow higher temperatures in muscle, allowing bacteria to grow more profusely and resulting in increasing degrees of burn in the deeper areas of the muscle mass.

The most reliable diagnostic method may be histopathologic examination of biopsy specimens obtained from deep muscle tissues, flash frozen, sectioned with a cryostat at the auction, stained and examined. All of this can be accomplished in 0.5-1 hour. With the exception of tests made on blood samples collected at the time of catching, biochemical tests were not useful in prediction and diagnosing the burnt tuna condition of unquartered tuna.

A stress-induced abnormality which occurs in hog muscle known as porcine stress syndrome (Winstanley, 1979) seems similar in some characteristics to burnt tuna. Both conditions result in pale and soft muscles. It is possible that there may be related causes for the two conditions.

It is obvious that further studies on burnt tuna are necessary. The small number of fish sampled in this study (12) resulted in possible leads and solutions, but precludes strong and definitive statements on this condition. It is likely that improved handling and chilling procedures from the time of capture may help to reduce the incidence of burnt tuna.

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Drug Immobilization of Walrus (*Odobenus rosmarus*)

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Five out of nine walrus (*Odobenus rosmarus*) were successfully immobilized at Round Island, Alaska, in May of 1978 by combinations of phencyclidine hydrochloride and acepromazine hydrochloride. A crossbow was an effective delivery technique. Walruses that had recently hauled out were more suitable for immobilization than well-rested animals. Care was taken to prevent walruses from overheating or suffocating.

Key words: walrus, *Odobenus rosmarus;* immobilization, marine mammal

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Grâce à des combinaisons d'hydrochlorure de phencyclidine et d'hydrochlorure d'acépromazine, on a pu immobiliser avec succès cinq sur neuf morses (*Odobenus rosmarus*) à l'île Round en Alaska en mai 1978. L'arbalète a été un instrument efficace de lancement. Il était préférable d'immobiliser des morses qui avaient atterri récemment plutôt que des animaux bien reposés. On s'est efforcé de prévenir l'échauffement ou la suffocation des animaux.

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IN this note the results of drug immobilization experiments on free-living walruses are reported. Immobilization may be necessary in future studies as walruses are too large and powerful to be restrained physically under field conditions.

From May 13 to May 21, 1978, we attempted to immobilize nine Pacific walruses (*Odobenus rosmarus divergens*) hauled out at Round Island, Alaska (58°36′N, 159°58′W, see Miller 1976 for description of island habitat). We used combinations of phencyclidine hydrochloride (Sernylan) and acepromazine hydrochloride (Lentfer 1969; Seal et al. 1970; Hofman 1975) in eight attempts, and one attempt was made with ketamine hydrochloride (Williams and Kocher 1978; Hunter et al. 1977). Our target dose range of 0.2–0.3 mg/kg of Sernylan was based on previous immobilization experiences with Weddell seals (Hofman 1975) and walruses (F. H. Fay, University of Alaska, Fairbanks, Alaska, personal communication). Initially we used a capture rifle (Lentfer 1969); however, the report of the rifle disturbed the walruses. In the last six immobilization attempts we used a crossbow to deliver the drugging darts. (Darts were attached to the arrow with Palmer Chemical Company arrow adapters.) Animals were approached within 25 m. Care was taken to be quiet and to remain out of sight during the approach. The occurrence of large boulders on the beach made the approach considerably easier. Only animals that were considered to be sleeping were used as subjects. Animals were darted either in the rear flank or in the front shoulder with a 3.5 in-barbed needle. There were no indications that the capture dart ever failed to fire or that the needles were too short to inject the drugs directly into muscle tissue.

Typically, the animal's reaction to the dart involved rearing the head back and looking around. As long as the rest of the herd was calm, the darted animal would not move into the water. In the three cases where the capture rifle was used, instead of the crossbow, the animal's reaction was to move

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TABLE 1. Summary of data related to immobilization of walrus on Round Island, Alaska.

Animal no.	Drug	Dose (mg)	Estimated weight (kg)	Estimated dose/weight (mg/kg)	Latent period (min)	Effect
1	Ketamine	900	1100	0.8	—	After 47 min animal went in water. Ineffective dose.
2	Sernalyn	250	1100	0.2	22	Animal lightly sedated. After 56 min animal mobile (went in water).
3	Sernalyn Acepromazine	375 10	1700	0.2	—	Animal immediately went in water.
4	Sernalyn Acepromazine	350 15	1600	0.2	35	Animal moderately sedated. After 1 h 59 min animal awkwardly mobile.
5	Sernalyn Acepromazine	325 15	1600	0.2	40	Animal lightly sedated, able to move head while being worked. After 1 h 45 min animal mobile.
6	Sernalyn Acepromazine	340 15	1600	0.2	33	Animal moved down beach, before becoming immobile. After 50 min one convulsion occurred and the animal died.
7	Sernalyn Acepromazine	450 5	1350	0.3	20	Animal heavily sedated. After 4 h 7 min animal mobile.
8	Sernalyn Acepromazine	360 15	1100	0.3	38	Animal moderately sedated. After 4 h 23 min animal mobile.
9	Sernalyn Acepromazine	360 10	1100	0.3	26	At 33, 39, and 41 min after injection convulsions occurred. After 3rd convulsion animal died.

towards the water's edge, and often animals near the darted individual were disturbed. We noticed that animals that were at the landward edge of the herd did not move as close to the water when they were disturbed as did animals that were at the center of the herd. We also noticed, after many unsuccessful stalks, that individuals that had been hauled out for several days were very difficult to approach without disturbing them. On the other hand, animals that had recently returned to the island to haul out were quite easy to approach. This may also be confounded by the cyclic nature of hauling patterns. In general, the number of hauled out animals would cycle from thousands of animals to a few animals in roughly a 10-d period. During the buildup, the herds were large and animals were easy to approach. During the decline phase, herds were generally smaller, and animals were much more difficult to approach.

Four different combinations of drugs and dosage were tried (Table 1): ketamine (0.8 mg/kg); Sernylan (0.2 mg/kg); Sernylan (0.2 mg/kg) and acepromazine (0–15 mg); and Sernylan (0.3 mg/kg) and acepromazine (5–15 mg). The ineffective dose of ketamine was the maximum that could be delivered by a single dose, and therefore, further experiments with ketamine were discontinued.

The symptoms associated with Sernylan and Sernylan/acepromazine injections were similar to those described by Hofman (1975) for Antarctic seals. We observed an increase in nasal secretions and tear formation (first effect), resting of the head on the tusks (second effect), and the lack of response to mechanical stimulation (third effect). An animal was considered lightly sedated if it could still move its head slightly while being handled. With light sedation, eye reflexes were good and breathing was regular (8–15 breaths per minute). A moderately sedated animal had no head control, good eye reflex, and a breathing rate between five and seven breaths per minute. A heavily sedated animal had no head control, a very weak eye reflex, and a breathing rate of two to four breaths per minute. Lightly sedated animals were mobile within 2 h after immobilization; moderately sedated animals were mobile between 2 and 4 h after immobilization; and heavily sedated animals were only awkwardly mobile between 4 and 7 h after immobilization.

Thermoregulation is disrupted by Sernylan (Seal et al. 1970), and heat stress may have occurred in animals immobilized for more than several hours on warm, sunny days (daytime temperatures reached 15°C during the study period). We attempted to minimize this problem by pouring cold water over heavily sedated animals. Heavily sedated animals with weak eye reflex were also exposed to possible eye damage from flies that occur on the hauling grounds. Another potential problem is the position of the immobilized animal relative to the slope of the beach. The two fatalities that occurred involved animals that moved toward the water's edge prior to complete immobilization. This positions the head and chest lower than the abdomen. The resulting pressure of the abdominal viscera on the diaphragm may have inhibited the respiration of the drugged walruses. We feel this was not simply an overdose of the drug because both animals were mobile just prior to when their breathing stopped. Most hauled out walruses lay facing up the incline of the beach, which may facilitate breathing.

We believe that additional immobilization experiments should be conducted. Our results indicate that a dose of 0.2−0.3 mg/kg of Sernylan is a reasonable dosage, but because of respiratory depression, alternatives to phenothiazine compounds should be considered (e.g. valium). Sernylan is not currently available and other immobilizing agents presumably must be used in the future. Based on our observations, future researchers, in developing adequate immobilization techniques for walrus, should consider the importance of delivery techniques, the sensitivity of walruses to Sernylan, and the potential problem of overheating. We recommend the crossbow as a reliable means of projecting the drugging darts, and caution against attempting immobilization research where the slope of the terrain is not level. In addition, we recommend that researchers, when choosing individuals to immobilize, select individuals that have recently hauled out and are part of a large herd.

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Estimating the Average Age of First Birth in Marine Mammals

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The average age of sexual maturity and the average age of first birth should not be estimated with identical models. The two parameters often differ by at least 1 y because, among marine mammals, ovulation and parturition take place in different years because of the relatively long gestation period. Furthermore, the assumptions necessary to estimate the average age of sexual maturity cannot be made to fit the data used to estimate the age of first birth. Equating the two models is essentially equivalent to assuming that each ovulation will result in a birth. The described procedure lends itself well to age-specific data. Comparisons between populations should be with a Chi-square goodness-of-fit test.

Key words: reproduction, marine mammals, sexual maturity

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On ne devrait pas se servir des mêmes modèles pour estimer l'âge moyen de maturité sexuelle et celui de la première parturition. Souvent, les deux paramètres différent d'au moins un an parce que, chez les mammiféres marins, l'ovulation et la parturition ont lieu dans des années différentes par suite d'une période de gestation relativement longue. En outre, les hypothèses nécessaires à l'estimation de l'âge moyen de maturité sexuelle ne peuvent être adaptées aux données utilisées pour estimer l'âge de première parturition. Égaliser les deux modèles équivaut essentiellement à supposer que chaque ovulation aboutira à une naissance. Le mode opératoire décrit ici se prête bien à des données spécifiques à l'âge. Les comparaisons entre populations devraient se faire par le test du khi carré.

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FOR many species of marine animals, ovarian and tooth specimens are available, which can be used to generate the average age of sexual maturity (DeMaster 1978a; Laws et al. 1975). When using DeMaster's (1978a) model to estimate the average age of sexual maturity, one necessarily assumes that animals that have not ovulated at age x have not ovulated before age x. One must also assume that animals that have ovulated at age x will ovulate every year thereafter. These two assumptions are often true for pinnipeds (Chapman 1973; DeMaster 1978b; Laws 1956; Oritsland 1970; Sergeant 1966; Smith 1973; and Stirling 1971) and the sea otter (*Enhydra lutra*; A. Johnson, NFWL, 4454 Business Park Blvd, Anchorage, AK, personal communication). However, for species like the walrus (*Odobenus rosmarus*; Burns 1965; Fay 1955), the polar bear (*Ursus maritimus*; Lentfer 1976; Lentfer et al. 1981), and most cetaceans, the long period of gestation and nursing precludes annual ovulations. Therefore, to estimate the age of sexual maturity in animals that do not ovulate annually with the procedure described by DeMaster (1978a), only those animals that were "available" for breeding (that is, without young or at the point in maternal care where mating usually takes place) should be included in the estimate.

For species of marine mammals where data on reproductive success are derived from the presence or absence of live young or fetuses, the assumptions of the model used to estimate the age of sexual maturity (DeMaster 1978a) are not reasonable. That is, animals that have not given birth at a given age could have given birth previously, and animals that have given birth at age x cannot be assumed to give birth at all subsequent ages. In this paper a method is described that is appropriate for estimating the average age of first birth for marine mammals for which data on the presence or absence of live young or fetuses are available. However, it should be remembered that only animals that are "available" for reproduction should be considered in the analysis.

The average age of first birth is estimated as follows:

$$(1) \quad \hat{y}(x) = t(x)/n(x)$$

where x = the age of the female,
$\hat{y}(x)$ = the estimated proportion of females of age x that are reproductive,

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$t(x)$ = the number of females of age x that are pregnant or with young of the year, and
$n(x)$ = total number of females of age x observed.

The estimated probability of giving birth at or before age x, $z(x)$, is

$$(2) \quad \hat{z}(x) = \hat{y}(x) + [1 - \hat{y}(x)]\,[\hat{z}(x - 1)].$$

The probability of giving birth for the first time at age x, $r(x)$, plus the probability of giving birth at or before age $x - 1$, $z(x - 1)$, equals $z(x)$. Thus, the estimated probability of reproducing for the first time age age x is

$$(3) \quad \hat{r}(x) = \hat{z}(x) - \hat{z}(x - 1).$$

The average age of first birth is then estimated by:

$$(4) \quad \bar{x} = \sum_{x=0}^{w} x\,\hat{r}(x),$$

where w = the minimum age where $z(x) = 1.0$.

The derivation of this procedure necessarily assumes that the probability of reproducing at age x is independent of the probability of reproducing at age $x - 1$, given that the adult female was available in both years. For data where individuals are only included once in the analysis, this assumption should be satisfied. For many species, $y(x)$ will be independent of $z(x - 1)$ after a threshold age is reached (DeMaster 1978b) and for these animals, including resightings of the same individual, should not significantly bias the estimate of $r(x)$. It is also assumed in this estimation procedure that $\hat{y}(x)$ and $\hat{z}(x)$ are unbiased estimates of $y(x)$ and $z(x)$.

The estimated variance of the average age of first reproduction is derived as follows (equations 6, 7, and 8 are derived by use of the Delta method, Seber 1973).

$$(5) \quad \text{var}\ \hat{y}(x) = \frac{\hat{y}(x)\,[1 - \hat{y}(x)]}{n_x - 1}$$

$$(6) \quad \text{var}\ \hat{z}(x) = \text{var}\ \hat{z}(x - 1) + \text{var}\ \hat{y}(x) + [\hat{y}(x)]^2\ \text{var}\ \hat{z}(x - 1) + [\hat{z}(x - 1)]^2\ \text{var}\ \hat{y}(x)$$

$$(7) \quad \text{var}\ \hat{r}(x) = \text{var}\ \hat{z}(x) + \text{var}\ \hat{z}(x - 1)$$

$$(8) \quad \text{and var}\ (\bar{x}) = \sum_{x=0}^{w} x^2\ \text{var}\ \hat{r}(x).$$

The derivation of the variance of $\bar{x}$ assumes that $\hat{z}(x - 1)$ and $\hat{y}(x)$ are independent, that var $\hat{z}(x)$ and var $\hat{z}(x - 1)$ are independent, and that the var $\hat{r}(z)$'s are independent. These assumptions should be met if the previous assumption that the $y(x)$'s are independent is met.

Table 1 (hypothetical data) presents this precedure as it is used to estimate the average age of first birth and the variance associated with this average. DeMaster (1978a) estimated the average age of sexual maturity with this same data set. Under the assumptions for determining the age of sexual maturity, the age of first birth is overestimated ($\bar{x} = 3.34$ vs. $\bar{x} = 3.09$). These assumptions are equivalent to assuming that each ovulation will result in a birth. This overestimate occurs because the probability of giving birth at or before age x, ($z(x)$), under the assumptions of the sexual maturity model ($z(x) = t(x)/n(x)$: DeMaster 1978) is always less than or equal to the estimated $z(x)$ under the assumptions appropriate for estimating the age of first birth (equation 2). Therefore, using the equations appropriate for estimating the age of sexual maturity on data concerning the presence or absence of young or fetuses has the effect of increasing the probability of giving birth for the first time at the older ages relative to the younger ages, which subsequently inflates the estimated age of first birth. A second problem with not distinguishing between the age of sexual maturity and first birth is that for many marine mammals the age at which mating and parturition takes place differs by at least 1 y. This difference exists because the gestation period in most marine mammals is in excess of 8 mo (Asdell 1964). Therefore, the age of sexual maturity and the age of first birth should be clearly distinguished because the assumptions for the two estimates are different, and because the age of the animal when it is sexual mature is often different from the age of the animal when it first gives birth.

TABLE 1. Calculation of the average age of first birth in a hypothetical population of females. Average age of first birth equals 3.092 yr, SE (x) = 6.77 yr.

Age in years, (x)	No. females observed, $n(x)$	No. females with young, $t(x)$	Proportion of reproductive females, $y(x)$	P (give birth at or before age x), $z(x)$	P (1st birth at age x), $r(x)$	$x\,r(x)$
0	35	0	0	0	0	0.0
1	30	6	0	0	0	0.0
2	25	6	0.24	0.240	0.240	0.480
3	20	13	0.65	0.734	0.494	1.482
4	20	16	0.80	0.947	0.213	0.852
5	15	12	0.80	0.989	0.042	0.210
6	15	12	0.80	0.998	0.009	0.054
7	10	8	0.80	1.000	0.002	0.014
8	10	8	0.80	1.000	0.000	0.0
						3.092

Estimating the average age of first birth in practice will involve at least one other assumption. In cases where the number of adult females with live young is used, one must assume that the mortality rate of the offspring from birth until it is seen with its mother is negligible. In cases where adult females are classified as pregnant or not, one must assume that intrauterine mortality is negligible. In this situation, it is probably best to use for the age of the adult female the age at parturition, and not the current age.

Another point that should be considered is how senescene may affect the estimated average age at first birth. In practice, the decline in reproductive success with age will not affect the estimate because this reduction in $y(x)$ occurs well past the age where $r(x)$ equals 1.0.

A simultation analysis of this procedure suggests that with sample sizes of roughly 125 animals in each age-class for which $r(x)$ is not zero, differences of 3 yr between populations will be detected. Therefore, for most studies where at least five indeterminant ages (ages where $0 < z(x) < 1.0$) will be encountered at least 600 "available" individuals will have to be sampled to obtain a confidence interval of 3 yr (95% confidence interval = $1.96\, x\, [\mathrm{var}\, (\bar{x})]^{0.5}$). In most studies this sample size is unrealistic. In many situations a comparison between two populations or between one population at two different times is more useful than a confidence interval. The categorical nature of this type of data lends itself well to contingency table analysis, and eliminates the assumption of normalcy that is associated with ANOVA tests. Therefore, a contingency table analysis is recommended for comparing two different populations or one population at two different points in time because it will be more sensitive to differences than the standard t-test.

The estimation procedure described in this note should be particularly useful in mark–recapture studies where data on production of young are available, but accompanying ovarian data are not available. Where ovarian data are available, the average age of sexual maturity will be more sensitive to differences between populations than the average age of first birth for similar sample sizes.

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TWENTY

Incorporation of Density Dependence and Harvest into a General Population Model for Seals

DOUGLAS P. DEMASTER

INTRODUCTION

Population models constructed in an attempt to simulate the behavior of real populations of seals have historically incorporated convenient and sometimes arbitrary mathematical functions that have mathematically derived equilibria. At present, it is impossible to know what mathematical function best describes the form of the density dependence responses that are assumed operative in nature. Various functions have been applied (Chapman, 1961, 1973; Fowler and Smith, 1973; Allen, 1975; Lett and Benjaminsen, 1977; Eberhardt and Siniff, 1977), but until recently (Fowler, 1981; Chapter 23) no clear patterns have emerged. The various functions do seem to form a continuum ranging from conservative linear functions (Allen, 1975), to nonlinear functions (Eberhardt and Siniff, 1977; Fowler, 1981; Chapter 10). Differences are related to the degree of density dependence expressed at any particular density, with linear functions having a gradual and consistent depressing effect on reproduction or survival when compared to nonlinear functions which concentrate changes into certain ranges of population levels. Therefore, simulation with linear and nonlinear functions should produce a range of types of population responses that should bracket the true population response in nature. Also, many population models assume that the age structure of the harvest has little or no effect on the predictions of the model (but see Chapter 23). In addition, many population models ignore the fact that density dependence may be restricted to specific age classes with reproduction and survival of other age classes being essentially density independent (at least over the observed range of densities). If only those age classes beyond the ages in which reproduction and survival are density dependent are harvested, then it is conceivable that harvest mortality may not give rise to strictly compensatory responses (Brownie et al., 1978). Finally, some population models that incorporate density dependence are based on the assumption that the regulatory mechanisms are operative throughout the entire year. Some evidence exists that this is not the case for Weddell seals (DeMaster, 1978). It appears that, for this species at least, regulatory mechanisms are only operative at specific and predictable times of the year. The purpose of this chapter is to investigate the ways several factors influence the dynamics of a population of Weddell seals as represented by a collection of assumptions in the form of a population model. These include (1) changing the density-dependent functions from linear to nonlinear form, (2) changing the age at which survival is density dependent (from pups to adults), (3) changing the age structure of the harvest from a harvest of pups to a harvest of adults, and (4) changing the time of the harvest. The latter allows early density-dependent harvest compensation (to be defined later) to occur in one case but not in another.

A PROJECTION MATRIX

A 25 × 25 projection matrix (Leslie, 1948) may be used for representing a population of female Weddell seals with 25 age classes. As constants, the entries of the top row (age specific reproduction as females born per female) were: $b_0 = b_1 = b_2 = 0$; $b_3 = 0.10$, $b_4 = 0.25$, $b_5 = 0.30$, $b_6 = 0.35$, and $b_7 = b_8 = \cdots b_{24} = 0.38$, as derived from DeMaster (1978), Siniff et al. (1977), and Stirling (1971). Similarly, the subdiagonal entries (age-specific survival) may all be set equal to 0.85 (DeMaster, 1978). Such a matrix model, with constant parameters, produces a constant growth rate and age structure (Leslie, 1945).

A more realistic approach involves a similar model that incorporates some type of density dependence into the transition matrix (Leslie, 1948; Fowler and Smith, 1973; Fowler and Barmore, 1979). Such density dependence is often assumed to be linear (Allen 1975), even though there is growing evidence to support nonlinear functions for large mammals in general (Fowler, 1981; and Chapter 23). In this analysis the following four density-dependent functions were used:

$$P_0 = A - M_0 X_1 \tag{1}$$

$$P_0 = A\,(1 - e^{-B(X_k - X_1)}) \tag{2}$$

$$P_i = A - M_1 X_2 \qquad i = 1, 25 \tag{3}$$

$$P_i = A(1 - e^{-\mathrm{B}(X_K - X_2)}) \qquad i = 1, 25 \tag{4}$$

where P_0 = annual pup survivorship

P_i = annual survivorship of seals i years old

A = maximum annual survivorship

M_0 = constant associated with the number of female pups and their survivorship

M_1 = constant associated with the number of females 4 years of age or older and their survivorship

X_1 = number of female pups

X_2 = number of females 4 years of age or older

B = a constant that describes the shape of the curve in equations (2) and (3)

X_k = the maximum number of female pups in the population

X_K = the maximum number of females 4 years of age or older in the population

The following values were used in the 22 simulations summarized in Table 1: $A = 0.85$; $M_0 = 0.000125$; $M_1 = 0.00003594$; $B = 0.02$; $X_k = 350$; $X_K = 1000$. The estimated maximum annual survivorship A is a value derived from the available empirical data (DeMaster, 1978). X_k and X_K were approximated by the maximum number of pups and adult females that have previously been recorded in the McMurdo Sound study area (DeMaster, 1978). The value of B was arbitrarily set equal to 0.02 (Eberhardt and Siniff 1977) and represents a relatively rapid change in the shape of the nonlinear function (Figure 1). M_0 was determined by simulating the population with the nonlinear form of pup survivorship until an equilibrium was reached, and then using the equilibrium values of P_0 and X_1 to solve for M_0 (Figure 1). A similar approach was used to solve for M_1.

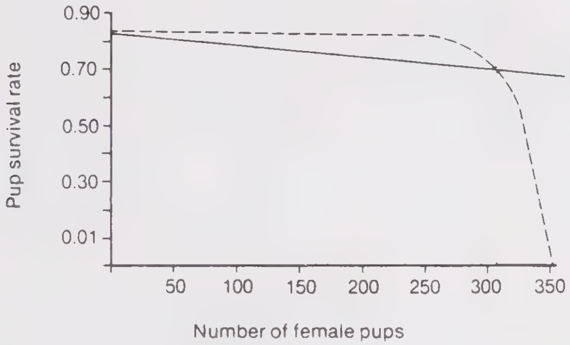

Figure 1 Linear (solid line) and nonlinear (dashed line) relationships between the survival rate for pups and the number of female pups born. The linear form is fit through the initial point (0, 0.86) and the equilibrium point (308, 0.69). Dotted line shows equilibrium level of female pups born.

The simulation was allowed to continue until an equilibrium was reached or until the population went extinct as was done by Fowler and Smith (1973) and Allen (1975):

$$X_{t+1} = L(X_t)X_t - H_t \tag{5}$$

where X_{t+1} = the 25 × 1 population vector for year $t + 1$

$L(X_t)$ = the 25 × 25 variable projection matrix expressed as a function of X_t

X_t = the 25 × 1 population vector for year t

H_t = the 25 × 1 harvest vector in year t

The original population vector was derived from Stirling (1971) and DeMaster (1978):

Age	Frequency	Age	Frequency
1	232	10	44
2	179	11	37
3	152	12	30
4	130	13	26
5	108	14	22
6	90	15	18
7	75	16	15
8	63	17	12
9	53	18	10

At each iteration of the model, a new population vector is calculated. Appropriate portions of the new population vector are then used to calculate the entries for the projection matrix using various combinations of equations (1)-(4). Thus, the influence of changing the form of the density-dependent function and the age at which survival is density dependent can be investigated. By changing the harvest vector from one containing all pups to a vector of only seals 4 years of age or older (harvest from each age class was proportional to the size of the particular age class), the influence of varying the age structure of the harvest can be investigated.

Equation (5) is representative of a situation where the harvest occurs after the age-specific survival and reproduction have been realized. If the harvest occurs after the rates of survival and reproduction have been determined, there is no chance for further compensation by the nonharvested segment of the population during that unit of time. In other words, there is no increase in the rates of reproduction or survival as a result of the removal of a segment of the population by harvesting. Such reactions, by necessity, can occur only in the next time step. This may or may not be a realistic situation. It is possible that populations may react to the density immediately following harvest (rather than prior to harvest) thus compensating for the harvest in the same time step (a reversal of the situation above). To determine the influence that any such harvest compensation may have on the equilibrium population a simulation that calculated the harvest before the projection was also investigated. This is represented in equation form as:

$$X_{t+1} = L(X_t)(X_t - H_t) \tag{6}$$

In this case, the entries for the projection matrix are calculated from the population vector subsequent to the harvest.

The simulations of female Weddell seal populations, as produced for this study (Table 1), can be broken down into three categories. These are (1) simulations with no harvest (Table 2), (2) simulations in which only pups are harvested (Table 3), and (3) simulations in which only animals 4 years of age and older are harvested (Table 4). Cases 1 and 2 and cases 3 and 4 must necessarily be equivalent in all ways at equilibrium because of the way in which the slope of the linear form of the density dependence was derived. Cases 5 and 6 (Table 2) incorporated both adult and pup survivorship that was density dependent. In these cases, the equilibrium population and number of female pups are not the same. This is because the equilibrium survival rates (P_0/P) are not associated with the same number of female pups and the number of adult females for the linear and nonlinear models.

Table 1 **Summary of 22 Simulations**

Case	P_0	P	Harvest Compensation	Composition of Harvest
1	Linear	—	No	0
2	Nonlinear	—	No	0
3	—	Linear	No	0
4	—	Nonlinear	No	0
5	Linear	Linear	No	0
6	Nonlinear	Nonlinear	No	0
7	Linear	—	No	Pup
8	Nonlinear	—	No	Pup
9	—	Linear	No	Pup
10	—	Nonlinear	No	Pup
11	Linear	Linear	No	Pup
12	Nonlinear	Nonlinear	No	Pup
13	Linear	—	Yes	Pup
14	—	Nonlinear	Yes	Pup
15	Linear	—	No	Adult
16	Nonlinear	—	No	Adult
17	—	Linear	No	Adult
18	—	Nonlinear	No	Adult
19	Linear	Linear	No	Adult
20	Nonlinear	Nonlinear	No	Adult
21	—	Linear	Yes	Adult
22	—	Nonlinear	Yes	Adult

RESULTS OF SIMULATIONS

The results of simulations without harvest (Table 2) show that different density-dependent mechanisms will produce different equilibrium populations. Dif-

Table 2 Results of Weddell Seal Population Simulation in Which There Is No Harvest[a]

Case (see Table 1)	Population	X_1	P_0/P	Mean Age	Time to Return (20% reduction)
1. Linear P_0	1701	308	0.6937	5.05	250
2. Nonlinear P_0	1701	308	0.6936	5.06	90
3. Linear P	1790	301	0.8202	4.51	230
4. Nonlinear P	1790	302	0.8201	4.51	50
5. Linear P_0 and P	893	156	0.7708/0.8346	4.76	170
6. Nonlinear P_0 and P	1666	290	0.7715/0.8347	4.76	40

[a] See Table 1 and text for details concerning the nature of the model in each case.

ferent levels of pup production will be associated with these equilibrium populations. The largest difference in equilibrium occurred between cases 4 and 5. When both pup and adult survival are linearly density dependent, the number of pups and adults has to be substantially lower to reach equilibrium than when only one of these density-dependent mechanisms are employed. It is interesting that when only the survival of pups (P_0) is density dependent its equilibrium is less than when only the adult survival is density dependent. This is due to the differences in the composition of the resulting populations in the two cases, as explained in Chapter 23.

Changing the age classes subject to density-dependent survival thus has a predictable effect on the mean age of the equilibrium population. The same is true for the time necessary for the population to return to the equilibrium. When the survival of pups is density dependent, the mean age of the equilibrium population is greater than the mean age of the population when the survival of both pups and adults are density dependent. Also, when survival for all age classes is density dependent, the mean age at equilibrium is greater than when the survival for adults alone is density dependent (see Chapter 21).

Estimates of the time necessary for the population to return to equilibrium were generated by reducing each age class of the equilibrium population by 20%, and then finding how long it took for the population to reach a constant mean age (determined by a predetermined and uniform criterion). The nonlinear models were found to return more rapidly than the linear models because the nonlinear models used in this study have essentially maximum rates of growth until they approach the maximum population, while the linear models have growth rates that are constantly declining as the population increases. The most rapid return took 40 years, while the slowest return took 250 years (Table 2). DeMaster (1978) documented a 50% reduction in the breeding population of the Weddell seal in McMurdo Sound between 1975 and 1976. Stirling et al. (1977) documented a 50% reduction in the number of ringed seals *(Phoca hispida)* in the western Canadian Arctic. Returning from such reductions, of course, would require even more time than indicated by these models.

With a pup harvest as part of the population model, the population giving rise to a maximum sustainable yield (MSYP) and the maximum sustained yield itself

Table 3 Results of Weddell Seal Population Simulation in Which There Is a Harvest of Pups[a]

Case		MSYP			Yield	Maximum	
(see Table 1)	MSYP[b]	Equilibrium	H_1	X_1	(%)	Population	H_1 max
7. Linear P_0	938	0.55	17	170	10	—	—
8. Nonlinear P_0	1396	0.82	43	253	17	—	—
9. Linear P	1018	0.57	14	177	8	—	—
10. Nonlinear P	1481	0.83	43	265	16	—	—
11. Linear P_0 and P	574	0.64	7	101	7	—	—
12. Nonlinear P_0 and P	1373	0.82	40	247	16	—	—
13. Linear P_0 compensation	1011	0.59	20	184	11	—	—
14. Nonlinear P_0 compensation	1665	0.98	52	301	17	1810	40

[a] See Table 1 and text for details concerning the nature of the model in each case.
[b] Population giving rise to a maximum sustainable yield (MSY).

(MSY) were determined by finding the equilibrium population at various levels of harvest. The largest harvest that the population could sustain was considered to be the MSY. By altering the form of the density-dependent function, the age at which it operates, and the time at which it operates, a range of corresponding MSYP were determined. The MSYP, expressed as a percentage of the equilibrium population (no harvest) was found to vary between 55 and 98 (Table 3). In general, if only the form of the density dependence was changed, simulations with nonlinear density dependence had higher MSYP than the models with linear density dependence. Similarly, nonlinear models tended to have higher MSY values when expressed as a percentage of the total pup production. A unique situation arose with nonlinear models in that some harvest rates actually increased the equilibrium populations (Table 3, case 14). In this case, harvesting 40 pups increased the survivorship of the remaining pups to such an extent that the equilibrium population of the model was 109 seals larger than the equilibrium population with no harvest at all.

Table 4 Results of Weddell Seal Population Simulation in Which There Is a Harvest of Adults[a]

Case (see Table 1)	MSYP	$\frac{\text{MSYP}}{\text{Equilibrium}}$	Harvest
15. Linear P_0	1166	0.69	7
16. Nonlinear P_0	1570	0.92	22
17. Linear P	831	0.46	10
18. Nonlinear P	1437	0.80	24
19. Linear P_0 and P	665	0.74	3
20. Nonlinear P_0 and P	1475	0.89	21
21. Linear P compensation	831	0.46	10
22. Nonlinear P compensation	1486	0.83	25

[a] See Table 1 and text for details concerning the nature of the model in each case.

When the age structure of the harvest is changed from exclusively a pup harvest to a situation in which all seals 4 years of age or older (approximate age of sexual maturity and subsequent return to breeding population: Stirling, 1971; Siniff et al., 1977) are harvested, the MSYP, when expressed as a percentage of the nonharvested equilibrium population, varied between 46 and 92 (Table 4). This is essentially the same as the range of MSYP for the pup harvests. The cases with adult harvests were similar to cases with pup harvests in that those with linear density dependence had lower MSY values and equilibrium populations than those with nonlinear density dependence. The maximum adult harvest occurred in the case where nonlinear density dependence of adult survivorship and harvest compensation were incorporated. In comparing the maximum yields for pup and adult harvests, roughly twice as many pups can be harvest from one age class as adults can be harvested from 21 age classes. This supports the prediction of Eberhardt and Siniff (1977) that marine mammal populations are extremely sensitive to increases in adult mortality.

The simulations that incorporated pup harvests of various types had MSY values that ranged from 7% (Table 3, case 11) to 17% (Table 3, cases 8 and 14) of the pup numbers. Comparable ranges were even greater when harvest of adults is included in the cases being compared. For all harvest strategies that were examined in this work the MSYP, given as a percentage of the nonharvested equilibrium population, varied between 46 and 98. This analysis suggests that reasonable management decisions must incorporate information concerning the regulatory mechanisms, harvest compensation, time at which density dependence is expressed, and the age structure of the harvest. Specifically, models and predictions for one species should not necessarily be accepted as general guidelines for the management of other species.

DISCUSSION

The Model

The main purpose of this chapter is to demonstrate the effects of different regulatory processes, types of harvests, and harvest schedules. Therefore, the particular hypothetical relationships used to model the regulatory processes can be considered only as rough approximations of what may actually happen. The four types of density dependence in equations (1)-(4) represent a wide range of reasonable types of density dependence. By examining the extremes of a reasonable spectrum of possibilities, minimum and maximum estimates can be produced to create an interval within which the true value will occur.

Other modes of regulation need investigating. Eberhardt (1977), for example, suggests that in addition to the survival of pups, age of first reproduction is a very important mechanism in the regulation of populations of marine mammals. For simplicity, age-specific reproduction was assumed constant in this model. This needs to be investigated. Some of the effects of changing this variable are examined by Fowler and Smith (1973), Fowler and Barmore (1977), and Eberhardt and Siniff (1977), and in Chapter 23. Preliminary modeling in this study suggested that manipulating the age of first reproduction may cause cyclic behavior (see May and Oster, 1976).

The particular nonlinear function used in this work is attractive because it comes close to approximating the concept of a threshold density. That is, survival, for example, is essentially density dependent only when density is above the threshold. Chapman's 1973 presentation of data on northern fur seals *(Callorhinus ursinus)* seems to support the threshold concept because recruitment was found to appear independent of density at low population levels. These are dynamics that conform to the general pattern described by Fowler (1981) and in Chapter 23. In this pattern, most density-dependent change is restricted to a range of levels close to the equilibrium for large mammals.

Models Without a Harvest

This analysis indicates that mechanisms that have relatively small effects on the growth rate of a population indeed may regulate those populations. However, the time necessary for this regulation to occur may be longer than the period during which environmental conditions are constant enough to allow for a constant equilibrium population. Because the minimum time necessary for the population to return to the equilibrium (after a 20% reduction in the population) was 40 years in this work, it seems unlikely that seal populations would ever reach a stationary age distribution (age distribution where age structure is constant). If it is assumed that declines can occur much more rapidly than increases (Stirling et al. 1977; DeMaster, 1978; Siniff et al., 1977; Payne, 1977), it may be that populations of pinnipeds will commonly be found to be increasing to a level their resources can maintain. However, periodically populations may rapidly decline, possibly owing to changes in some aspect of the physical environment. This type of growth pattern needs to be considered as far as future methodologies and research (see Fowler, 1981).

Considering the predictable manner in which the mean age of a population responded to various types of density dependence, it may be possible to use the change in the mean age of the population as it grows to infer something about the age class for which density-dependent mechanisms are operative. That is, if the mean age of the population increases as the population increases, it is most likely that density-dependent factors are affecting the younger age classes or the birth rate (see Chapter 21), and vice versa. This approach may not be particularly sensitive because of the relatively wide confidence interval around the mean age that is generated from a distribution of ages. However, such a technique has been used successfully with southern elephant seals (*M. leonina:* Laws, 1960) to determine the number of bulls to be culled. Further studies of this population parameter should be conducted.

Models Incorporating Harvest

The incorporation of age-specific harvests into a general population model seems to be necessary in light of the findings in this study and as shown in Chapter 23. The fact that the maximum sustainable yield of adult female Weddell seals was only 1.7% in the most liberal population model in this study suggests that harvests as low as 20 seals from a population of 1000 adult females may be critical. Since 1964, an average of 30 adult females have been harvested from the McMurdo population of Weddell seals in the Antarctic. This population contains roughly 1000 adult females. The 1977-1978 harvest of this population was roughly 35 adult females (combined take of United States and New Zealand). The gradual decline of this population since 1967 may be, in part, a result of this adult harvest (DeMaster, 1978).

On the other hand, harvesting 17% of the female pup production could be sustained by this same simulated population. It is even conceivable that some harvests may temporarily increase populations. A similar mechanism has been suggested for black bears (Kemp 1974).

Analyses that have incorporated factors similar to those discussed in this chapter have been presented by Stirling et al. (1976), Allen (1975), and Chapman (1961). Stirling et al. (1976) simulated brown bear and polar bear populations with a fixed age-specific rate of reproduction and survival. Although it is not possible to generate MSY values with their model, a type of sensitivity analysis can be generated. The authors found that various population projections were extremely sensitive to manipulations that affected the mortality of adult females.

Chapman (1961) estimates the MSY of 3-year-old male northern fur seals *(Callorhinus ursinus)* with two different types of density-dependent rates of recruitment. Both models are nonlinear, with one model producing an MSY of 45%, when the population of pups is 68% of the maximum population of pups. The other model produces an MSY of 46%, when the population of pups is 72% of the maximum pup population. The estimated MSY of 3-year-old fur seals is much greater than the estimated MSY of pup Weddell seals in this chapter. This is primarily because the intrinsic growth rate for fur seals is much larger than for Weddell seals. However, the population at which the MSY occurs for fur seals is bracketed by the estimates of the MSY population produced in this chapter for Weddell seals.

CONCLUSIONS

It is difficult to generalize from these results because of the hypothetical nature of the model and because each manipulation was associated with a unique MSY and equilibrium population. Estimates of the MSY were found to be higher for nonlinear than linear models, higher for pup harvests than adult harvests. These results are consistent with the general patterns described in Chapter 23. Models that incorporated harvest compensation produced higher MSY than models that did not.

The management of populations of pinnipeds is confounded by difficulties in assessing population levels, regulatory mechanisms, and controlling factors. The recent criticisms of the concept of MSY (Larkin, 1977) and the current use of the concept of optimum sustainable population (OSP) (Marine Mammal Commission, 1975) seem to stem from an awareness of how sensitive current MSY estimates are to changes in the marine community (particularly of fishery stocks) and changes in the age structure of the harvest. In the future, the population models that are used to estimate MSY values must incorporate these factors. Changes in the community structure will necessarily alter the equilibrium population of seals, and adjustment procedures need to be established. Perhaps initial carrying capacity estimates should be compared with current carrying capacity estimates. Perhaps, the effect of varying environments may have to be incorporated in future models by determining MSYs (stated as a percentage) in advance, but then delaying the determination of the quotas until an assessment of the current populations are made. Finally, the idea that one general model will predict maximum harvest rates and equilibrium stocks for many or all seals seems doubtful. For each species, the regulating mechanisms, and controlling factors must be identified before MSYs can be derived. In addition, the age structure of any proposed harvests must be incorporated in management oriented models because this is critical in determining the MSY for any particular population.

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MAMMALIAN SPECIES No. 145, pp. 1–7, 3 figs.

Ursus maritimus.

By Douglas P. DeMaster and Ian Stirling

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Ursus maritimus Phipps, 1774

Polar bear

Ursus maritimus Phipps, 1774:185. Type locality Spitzbergen.
Ursus marinus Pallas, 1776:691. Type locality Arctic Ocean, Siberia.
Ursus polaris Shaw, 1792:7. Renaming of *marinus* Pallas.
Thallassarctos eogroenlandicus Knotterus-Meyer, 1908:182. Type locality pack ice off coast of eastern Greenland.
Th[alassarctos] labradorensis Knotterus-Meyer, 1908:183. Type locality Okak, Labrador.
?Thalassarctos jenaensis Knotterus-Meyer, 1908:184. Type locality Jena Island, Spitzbergen.
?Th[allassarctos] spitzbergensis Knotterus-Meyer, 1908:184. Type locality Seven Islands, Spitzbergen.

CONTEXT AND CONTENT. Order Carnivora, Family Ursidae. The genus *Ursus* includes three species. The living populations of *Ursus maritimus* are not divided into subspecies (Wilson, 1976), although one fossil subspecies is recognized (Kurten, 1964).

DIAGNOSIS. Typically the body of a polar bear is stocky but lacks a shoulder hump. Polar bears have a longer neck and smaller head than other ursids (Fig. 1). The combined length of the first and second molars is less than the palatal width.

GENERAL CHARACTERS. Fur color varies among white, yellow, grey, or almost brown, depending on season and light conditions. The nose and lips are black, as is the skin. Adult males weigh 300 to 800 kg and measure 200 to 250 cm in length from tip of nose to tip of tail. Adult females weigh 150 to 300 kg and their total body length is about 180 to 200 cm. It is not meaningful to give mean weights because there is a cline in size from Spitzbergen, where the bears are smallest, to the Bering Strait where they are largest (Manning, 1971). Presumably the cline is similar across the Soviet Arctic to the Bering Strait, but this has not been investigated. Cubs weigh roughly 0.6 kg at birth and 10 to 15 kg when they emerge from dens in March or April. In March, yearlings weigh between 45 and 80 kg, while 2-year-olds weigh between 70 and 140 kg. Females reach adult weight by year 5 and males between years 8 and 10.

The length of skull (Fig. 2) ranges from 353 to 412 mm in males and from 311 to 380 mm in females. For adults, the height at the shoulder varies from about 130 to 160 cm. The length of tail ranges between 76 and 127 mm (Uspenskii, 1977).

Polar bears have a plantigrade gait and five toes on each foot. The claws are not retractable and in adults are 5 to 7 cm in length. The forepaws are large and oarlike, as an adaptation for swimming.

DISTRIBUTION. Polar bears are circumpolar in distribution. The southern limits of their range are determined by the distribution of pack ice and annual landfast ice during winter (Fig. 3). The centers of six apparently distinct populations in the main polar basin are: Wrangel Island and western Alaska, northern Alaska, the Canadian Arctic archipelago, Greenland, Svalbard-Franz Josef Land, and Central Siberia (Parovschikov, 1964, 1968; Uspenskii, 1965; and Vibe, 1967; Lentfer, 1974a; Stirling et al., 1975; Jonkel et al., 1976). Discrete subpopulations exist within the Canadian Arctic archipelago and James and Hudson bays (Stirling et al., 1975, 1977, 1978, in press). Polar bears have been recorded as far as 88°N (Stefansson, 1913, 1921) and as far south as St. Mathew Island and the Pribilof Islands (Ray, 1971) in the Bering Sea, James Bay (Jonkel et al., 1976) and Newfoundland in Canada (Smith et al., 1975), and Iceland in the North Atlantic. In some areas, such as the Beaufort Sea, polar bears make extensive north–south migrations in relation to the position of the southern edge of the drifting pack ice (Frame, 1969; Stirling et al., 1975). In the polar basin and adjacent areas, polar bears spend the summer along the edge of the pack ice. Near islands or the mainland, they concentrate in bays that retain shore-fast ice. After breakup, most of the bears that are near islands spend the summer along the coastlines of these islands. Occasionally, adult males have been observed to climb snow-covered glaciers and ice caps. In Hudson Bay, bears go inland and endure the warmer weather by digging caves or pits down into the permafrost (Stirling et al., 1977). In winter, polar bears move to the southern edge of the drift ice, to the coastlines of islands, and to the northern edges of the continents after the annual ice forms in these areas. On the basis of available data, it appears that most pregnant females do not winter along the ice edge, but return to coastlines where suitable habitat exists to make dens for bearing their young. Lentfer (1975) has recorded apparent instances of maternity denning in the pack ice, but it is not yet clear to what extent this occurs. The long-term distribution of polar bears is governed by climatic changes which restrict or increase the amount of available habitat (Vibe, 1967). Climatic factors probably affect the distribution of maternity dens more than does any other aspect of the environment because pregnant females must have access to suitable denning habitat by late October or November.

FOSSIL RECORD. Polar bears are thought to have originated from a segment of the Siberian population of brown bears (*Ursus arctos*) which was isolated during the glacial advances of the mid-Pleistocene (Kurten, 1964). With the exception of the Western Canadian Arctic where brown bears have been seen on the sea ice and polar bears have been seen chasing caribou, the geographic ranges of polar bears and brown bears do not overlap. The dentition of polar bears reflects a rapid evolutionary shift from the heterodont dentition of other ursid types, toward more homodont cheek teeth, as in other aquatic carnivores (Hecht, 1963). Kurten (1964) and Manning (1971) agreed that extant populations of polar bears represent a single species. Kurten (1964) documented the last Pleistocene occurrence of the subspecies, *Ursus maritimus tyrannus*, which was much larger than recent fossils.

FORM. The pelage of the polar bear is made up of a thick layer of underfur (5 cm in length) and an abundance of tufted intermediate guard hairs (15 cm in length) (Uspenskii, 1977). The color of the fur varies mostly with the season of the year. After the molt the fur is often pure white. The yellowish shade often seen during the summer probably results from oxidation by the

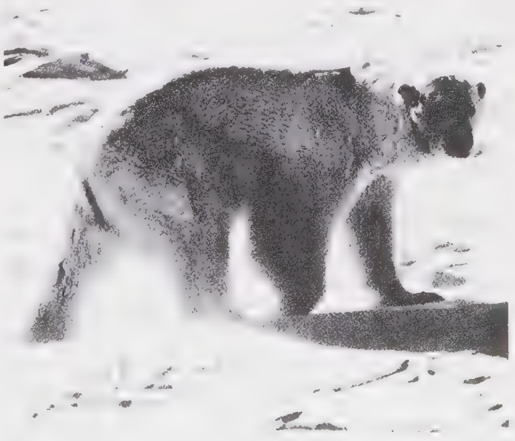

FIGURE 1. Adult male polar bear (*Ursus maritimus*). Photograph courtesy of H. P. L. Kiliaan.

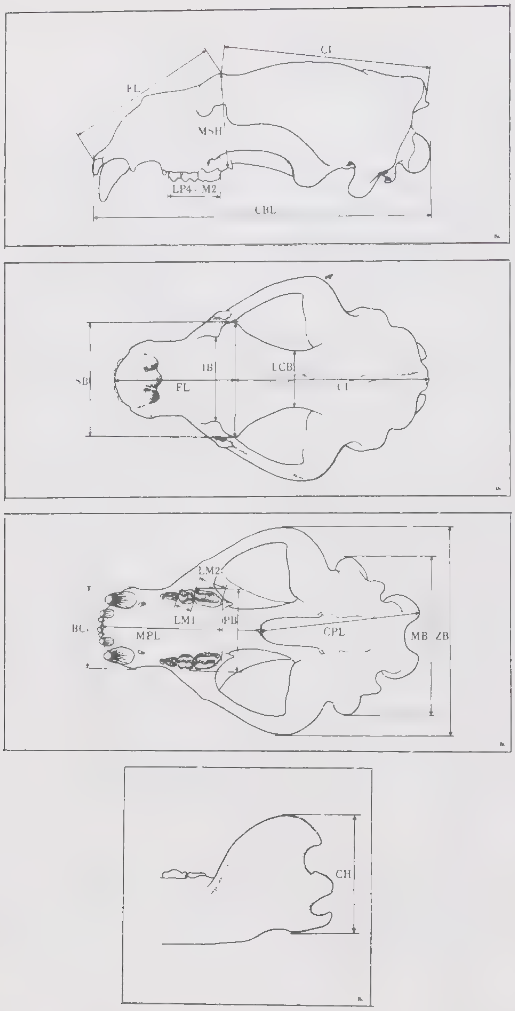

FIGURE 2. Polar bear skull (from Manning, 1971).

sun. Female polar bears have four functional mammae, two of which are 4 cm on either side of the midline of the belly slightly posterior of the axillae, and two of which are approximately 15 cm posterior to the anterior pair.

The dental formula is i 3/3, c 1/1, p 2-4/2-4, and m 2/3, total 38–42 (Banfield, 1974). Incisors are unspecialized and the canines are elongated, conical, and slightly hooked. The carnassial teeth are weakly developed. The first premolars are usually rudimentary. The fourth upper premolar does not have a third root (Stains, 1967). Sexual differences in the mandibular length were given by Larsen (1971) and molar measurements were reported by Gordon (1977). Polar bears can accumulate considerable amounts of subcutaneous fat. In adults, the thickness of this fat varies from 5 to 10 cm. Adult females are particularly fat just prior to denning.

Uspenskii (1977) described the musculature of a polar bear as powerful, with particularly well developed muscles in the posterior limbs and neck. The digestive tract is typical of carnivores, and apparently does not digest starches well. The stomach of an adult polar bear is large, with a capacity for more than 70 kg of food (Uspenskii, 1977).

The vitamin A content of the liver ranges between 15,000 and 30,000 units per gram (Rodahl and Moore, 1943; Rodahl, 1949; Lewis and Lentfer, 1967; Russell, 1967). This does not seem to vary with age or sex. A very high fatty acid content is characteristic of the polar bear liver, but the phosphate, lipid, and cholesterol contents are relatively low (Uspenskii, 1977). Uspenskii (1977) gave descriptions of the eyes and brain of the polar bear.

FUNCTION. The composition of polar bear milk has been described (Baker et al., 1963*a*, 1963*b*, 1967; Cook et al., 1970; Jenness et al., 1972). It contains more fat than whale milk, but less than seal milk (Jenness et al., 1972). The ash content was similar to that of other mammals and the sodium content was high compared to that of other milks (Jenness et al., 1972). An analysis of baseline blood parameters suggests that cubs have higher alkaline phosphatase and calcium levels than adults, and that an overall increase in blood glucose occurs in October and November (Lee et al., 1972). Cardiac physiology at rest and during exercise has been studied (Hock, 1968; Folk et al., 1970, 1973; Øritsland et al., 1976, 1977).

Øritsland (1969) presented data on hypothermia in polar bears and indicated that polar bears use both blubber and pelt for insulation. The oxygen consumption rate during walking increases at twice the rate of most mammals (Øritsland et al., 1976). Heat dissipation is accomplished through the foot pads and shoulders (conduction), and by panting (evaporative cooling) (Øritsland, 1970; Øritsland et al., 1974; Øritsland and Lavigne, 1976). Folk et al. (1972) described the physiology of two males that were held in captivity under conditions that induce denning in brown bears.

ONTOGENY AND REPRODUCTION. Spermatogenesis takes place from February to May, and possibly into June (Erickson, 1962; Lentfer and Miller, 1969; Lønø, 1970). In Alaska, paired bears have been observed in the field between 21 March and 10 May (Lentfer, 1976*a*). Lønø (1970) noted breeding pairs in Spitzbergen between 8 March and 20 June. Uspenskii (1977) reported that implantation is apparently delayed and gestation (conception to parturition) is therefore relatively long (195 to 265 days). Cubs are born in December and January in dens (Van de Velde, 1957, 1971; Lentfer, 1976*a*). Two young are commonly born in captivity (Kostyan, 1954), but estimates of average litter sizes from the wild vary between 1.58 and 1.87 (Lønø, 1970; Stirling et al., 1975, 1977; Lentfer, 1976*a*; Lentfer et al., in press). Geographic differences in litter size and dates of denning and den emergence seem to exist, especially between the Hudson Bay population and all other populations (Stirling et al., 1977). The sex ratio at birth appears to be equal. Newborn cubs have hair at birth (Blix and Lentfer, 1979), but are blind and weigh only about 0.6 kg. By the time they leave the den in late March or early April the cubs weigh approximately 10 to 15 kg. Geographic differences in the age of weaning may exist. Lønø (1970) suggested that cubs were weaned by 17 to 18 months of age, but this was not confirmed for animals of known age. Usually cubs are weaned at about 24 to 28 months of age (Stirling et al., 1975; Lentfer, 1976*a*), but cubs have been reported to be weaned after 3 years (Stirling et al., 1975). The earliest age of sexual maturity in females (as evidenced by pairing with males) is 3.5 years (Lentfer et al., in press). The average onset of breeding in the Beaufort Sea takes place between 5 and 6 years of age (Stirling et al., 1975; Lentfer et al., in press). Therefore, the average age at which the first cubs are produced is between 6 and 7 years of age, with individual females first reproducing at 4 to 8 years of age. In the eastern Canadian Arctic, however, the age of first breeding appears to occur at 4 years of age, one year earlier than average elsewhere (Stirling et al., 1978, 1980). The reason for this difference is not apparent. The age of reproductive senility for female polar bears has not been clearly determined, but reproductively active females of 21 years of age have been reported (Stirling et al., 1975; Lentfer, 1976*a*). Females tend to be in peak reproductive condition between the ages of 10 and 19 years, and exhibit a lower natality rate beyond age 20 (Stirling et al., 1978). The mean time span between litters for polar bears in the western Beaufort Sea is 3.6 years (Lentfer et al , in press). The mean of eight known reproductive cycles, calculated from females who were captured and recaptured with different litters of cubs, was 3.1 years and ranged from 2 to 4 years with a median and modal value of 3 (Lentfer, 1976*a*). An estimate of the annual rate of reproduction for polar bears can be made by assuming that females between 6 and 18 years of age have an average litter size of 1.7 (Stirling et al., 1975, 1978), a sex ratio at birth of 1:1, and an average reproductive interval of 3.1 years, which results in an average annual rate of reproduction of 0.274 females per adult female.

Based on the presence of mature sperm in the testes and

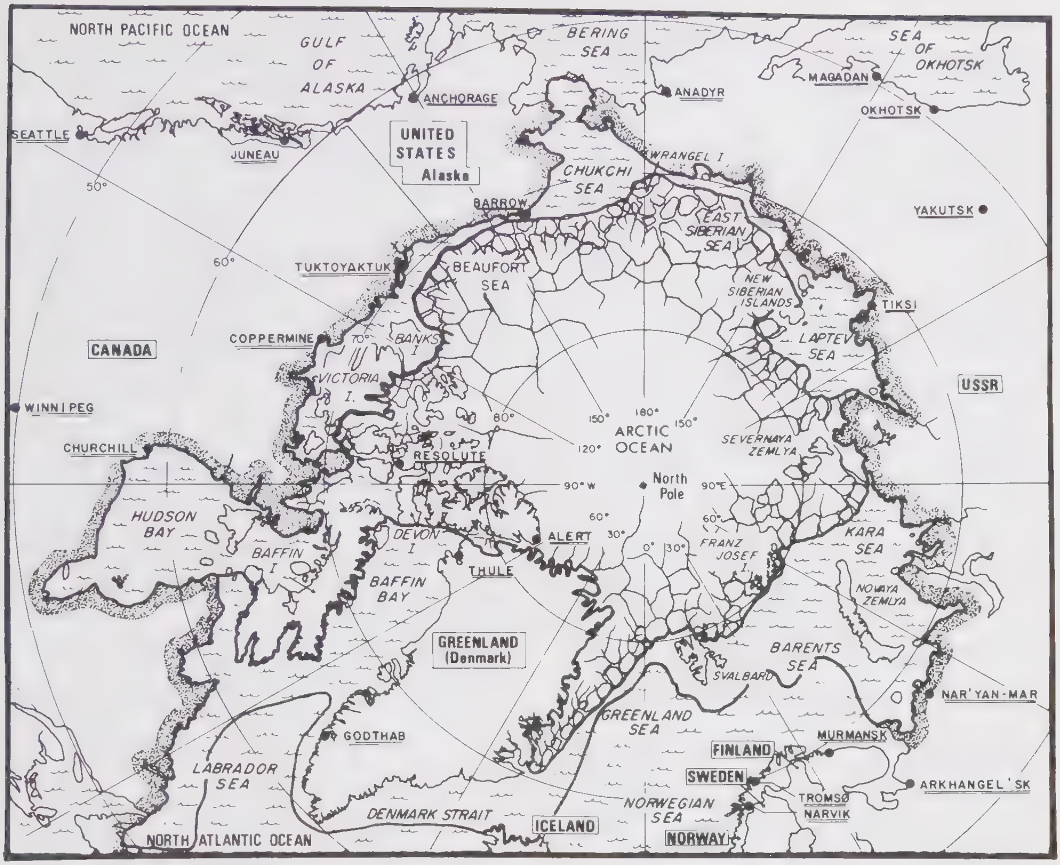

FIGURE 3. Distribution of polar bears. Their range is closely coupled to the distribution of polar sea ice. The inner dark line represents an average summer range of polar bears. The outer dark line represents an average winter range. The stipple pattern outside the winter range represents land areas which may be visited by female polar bears searching for den sites. Land areas enclosed by the winter range are also potential den sites. The ice cap is shown in an average summer position.

epididymis, the minimum and maximum age of breeding in males was estimated to be 3 and 19 years respectively (Lentfer and Miller, 1969). However, the presence of sperm does not necessarily indicate that copulation has occurred. Based on growth data alone (Kingsley, 1979), we suggest that it is unlikely that male polar bears mate before they are 6 years of age.

In Alaska, Lentfer (1976*a*) suggests that the maximum longevity for polar bears is between 20 and 25 years. Stirling et al. (1975) reported captures of animals 25 years of age, and estimated maximum longevity to be between 25 and 30 years. Age specific rates of survival are not precisely known. Mortality of adult males and females has been estimated to be between 8 and 16% (Stirling et al., 1976; Lentfer et al., in press). Typically, an annual mortality rate of 8 to 12% has been assumed (Stirling et al., 1976; DeMaster et al., 1980). Subadult mortality has been estimated between 3 and 16% (Lentfer et al., in press). The annual mortality of cubs prior to weaning is considered to be between 10 and 30% (Stirling et al., 1975; DeMaster and Stirling, in press).

ECOLOGY. Polar bears feed primarily on ringed seals, *Phoca hispida* (Stirling and Smith, 1975; Stirling and Archibald, 1977). The energetics of predation and caloric value of these seals were discussed by Stirling and McEwan (1975) and Best (1976). During spring at least half of the ringed seals killed by polar bears in the western Canadian Arctic are newborn pups (Stirling and Archibald, 1977). Bearded seals (*Erignathus barbatus*) are taken less often than ringed seals, but are important prey items. Polar bears also eat harp seals (*Pagophilus groenlandicus*) and hooded seals (*Cystophora cristata*); and scavenge on whale, walrus (*Odobenus rosmarus*) and seal carcasses (Russell, 1975; Heyland and Hay, 1976). Polar bears have been reported to prey on walruses, but polar bear mortalities have been attributed to walruses as well (Kiliaan and Stirling, 1978). Occasional references (Freeman, 1973; Heyland and Hay, 1976) have been made to polar bears attacking beluga whales (*Delphinapterus leucas*). Polar bears occasionally eat small mammals, birds, eggs, and vegetation when other food is not available (Russell, 1975). Scavenging on the remains of seals killed by polar bears is probably of great importance to the survival of arctic fox (*Alopex lagopus*) through the winter (Stirling and Archibald, 1977).

The diseases of polar bears have not been well documented. Roughly 60% of Alaskan bears harbor *Trichinella spiralis*, apparently contracted through eating infected seals (Lentfer, 1976*b*; Rogers and Rogers, 1976). The pattern of environmental contaminants in bears from western and northern Alaska was reported to be different, suggesting that these populations are relatively isolated from each other (Lentfer, 1974*a*, 1976*b*).

The population dynamics of polar bears vary geographically (Larsen, 1968; Stirling et al., 1975, 1977, 1978, 1980; Uspenskii, 1977; Lentfer et al., in press). Adult males (age 6 and above) comprise 12% of the Alaskan Arctic population (Lentfer et al., in press), 18% of the western Canadian Arctic (Stirling et al., 1975), and 17% of the Hudson Bay population (Stirling et al., 1977). Adult females comprise 26%, 19%, and 17% of these three populations, respectively. Cubs of the year, yearlings, and 2-year-olds constitute 32% and 26% of the Alaskan Arctic and western Canadian Arctic populations, respectively. Age composition reported from Alaska may include bias (Lentfer et al., in press) because a major portion of the sampling of natural populations was carried out in March and April when adult females with cubs of the year would be near their dens. Therefore, the number of cubs of the year and 6- or 7-year-old females has probably been undersampled relative to other age classes. However, in southeast Baffin Island, where ecological conditions are quite different, females with cubs of the year were not undersampled, but females with yearlings were (Stirling et al., in press).

Although estimates as low as 10,000 have been proposed by the Soviets (Uspenskii, 1977), the total number of polar bears is roughly estimated at 20,000 by Larsen (1972). The higher estimate was derived by assuming the current harvest of polar bears (roughly 1000 animals) is roughly 5 percent of the total population. Larsen (1972) also obtained a similar total by summing the regional estimates of polar bear populations.

In Alaska, polar bear densities have been estimated between 1 bear per 38 km^2 (Lentfer et al., in press) and 1 bear per 139 km^2 (Paul E. Tovey, unpublished report in file of author). The total population of Alaskan bears is estimated to be between 6000 and 9000 (D. G. Chapman, pers. comm.), and available evidence indicates that the population is stable or only slowly increasing (Lentfer et al., in press). In the western Canadian Arctic, where numbers have recently undergone large fluctuations owing to natural causes, the number of polar bears was estimated to be between 1000 and 1700 or 1 bear per 37 to 52 km^2 (Stirling et al., 1975, 1976). Estimates for the Soviet Union, Greenland, and Norway are not available, but populations are assumed to be stable or slightly increasing in Greenland and Norway, and stable or increasing, after recovery from previously reduced numbers, in the Soviet Union (Uspenskii, 1977).

The preferred habitat of polar bears is ice that is periodically active, where wind and sea currents cause movements and fracturing of the ice followed by refreezing. This process creates intermittent lanes or patches of recently refrozen ice (Stirling et al., 1975). This may occur at the interface between landfast ice and drifting pack ice, across the mouths of bays, or in tidal zones along coastlines. It is in this habitat that hunting success is highest (Stirling and Archibald, 1977).

Pregnant females leave the drifting pack ice in October or November to find suitable areas for denning. The relative discreteness of polar bear populations is therefore greatly influenced by the distribution and movements of the sea ice (Lentfer, 1971, 1972; Stirling et al., 1975, 1978). Pederson (1945) suggested that polar bears were all part of one circumpolar population. However, the results of recent tagging studies indicate that polar bears are divisible into relatively discrete populations (Jonkel, 1967; Lentfer, 1969, 1974*a*; Larsen, 1972; Stirling and Jonkel, 1972; Stirling et al., 1975, 1977, 1978, in press; Uspenskii, 1977). The sizes of the areas in which these poulations exist vary from relatively small areas in the Canadian Arctic to relatively large areas in the Chukchi Sea.

Currently, polar bears are protected under an international agreement (see Lentfer, 1974*b*) that restricts the taking of polar bears, and directs the signatory nations (U.S., USSR, Canada, Norway, and Denmark) to conduct research to identify the status of populations of polar bears and to protect the areas that are critical to the survival and reproduction of polar bears. In 1972, the U.S. Marine Mammal Protection Act ended responsibility of the State of Alaska for polar bear management. This act eliminated the non-native harvesting of polar bears, but allowed native subsistence hunters an unlimited take (subject to the condition that populations not become depleted). Presently, the state of Alaska has requested the return of management responsibility. In Canada only natives are allowed to hunt polar bears. The total hunting quota (719 for 1979–1980) is made up of individual quotas allocated to specific villages. These quotas are based on polar bear population data from each area. The economic value of this resource was described by Smith and Jonkel (1975*a*, 1975*b*), Smith and Stirling (1976), and Smith (1977, 1978, 1979). In Greenland, only residents are allowed to hunt polar bears. The annual take is estimated to be between 125 and 150 bears. In the Soviet Union and Norway, moratoria on taking polar bears were initiated in 1955 and 1973, respectively.

Handling of polar bears (Flyger et al., 1967; Larsen, 1968; Lentfer, 1968) for mark and recapture studies, plus the specimens available from local harvests have produced most of the data that are available on free-ranging polar bears (Lentfer, 1969; Larsen, 1972; Stirling et al., 1975, 1977, 1978, in press; Uspenskii, 1977; Lentfer et al., in press). In addition, radio telemetry studies using radio frequency transmitters and transmitters that are monitored via satellite have produced valuable information on movement patterns (Anderka et al., 1973; Kolz et al., 1978). Aerial surveys have not proven particularly successful (Scott et al., 1959; Larsen, 1972) but recent work with ultraviolet photography may enhance the success of aerial surveys (Lavigne and Øritsland, 1974).

Mark and recapture is the primary technique for estimating the abundance of polar bears (Stirling et al., 1975; DeMaster et al., 1980; Lentfer et al., in press), but information from guides has been shown to be a useful index of population size in Alaska (Lentfer, 1970). Population modeling has proven useful in evaluating the influence of various harvest strategies (Stirling et al., 1976), and indicates that a selective spring hunt of polar bears would be most beneficial to the maintenance of the population. Aging techniques for polar bears have been documented by Manning (1964), Stirling et al. (1975), and Hensel and Sorenson (in press). In general, the annuli found in the cementum produce the most reliable estimates of age, although they are more difficult to count in polar bears than in grizzly or black bears.

Polar bears have been successfully bred and reared in captivity (Jacobi, 1968; Wemmer, 1974; Nunley, 1977), but success depends on such factors as security, solitude, confinement to a small area, and a heated den (Jacobi, 1968). Dermatophilosis (Newman and Appelhof, 1965) and algal growth on the fur (Lewin and Robinson, 1979) have been described in captive bears.

BEHAVIOR. Behavioral studies of free-ranging polar bears have been limited to studies where high cliffs or observation towers were situated in areas used by polar bears (Stirling, 1974; Stirling and Latour, 1978). These studies suggest that during the summer, polar bears hunt seals primarily by still-hunting (77%) and stalking (23%). During the winter and early spring, almost all hunting is done by still-hunting (Stirling and Latour, 1978). Polar bears also stalk seals by crawling on the ice or swimming in the leads. In addition, the popular idea that polar bears cover their nose with a paw or push a chunk of ice with their nose while stalking seals has not been supported by observations of free-ranging polar bears (Stirling, 1974; Stirling et al., 1975). Cubs of all age classes (up to 2.5 years) do almost no hunting during late winter and early spring (Stirling and Latour, 1978). The duration of seal hunts by yearling and 2-year-old cubs were about the same, but the latter were significantly more successful at catching seals. Scavenging and intraspecific competition at seal carcasses were observed. Hunting and feeding behavior may be related to the caloric content of various prey items. During the spring, weaned seal pups and post-parturient females appeared to be preferred (Stirling and McEwan, 1975). Family groups tend to eat more of a seal kill than lone animals and more of the kill may be abandoned if the bear made a kill within the last day. In many instances, considerable portions of the prey items were not completely utilized, thus making scavenging an important consideration in the ecology of polar bears (Stirling, 1974). An important feature of feeding during the summer was grooming, where washing bouts typically occur after 30 minutes of feeding (Stirling, 1974).

The possible use of tools by bears to obtain food was reported by Kiliaan (1974).

Behavioral observations and mark-recapture data indicate that cubs remaining with their mothers until 2.5 years have a higher probability of survival than cubs weaned at an earlier age. Time budgets for the activities of polar bears were summarized in Stirling (1974) and Knudsen (1973, 1978). Polar bears have been reported to swim at least 40 miles across open water (Stirling, 1974), and are capable of diving under the ice and surfacing in the haul out-holes of seals (Stirling, 1974). Sleeping and resting were described by Stirling (1974). Bears are most active in the first ⅓ of the day, and least active in the last ⅓ of the day (Stirling, 1974). Adult females with young are not reported to be subordinate to bears of any other age or sex class, but adult females with cubs of the year are known to avoid interaction with adult males, presumably because of potential predation upon the cubs (Stirling, 1974). Polar bears seem to have a limited vocal repertoire and adult vocalizations are used primarily in aggressive interactions (Wemmer et al., 1976).

The density of maternity dens varies geographically (Uspenskii and Chernyavskii, 1965; Harington, 1968; Jonkel et al., 1972, 1976; Uspenskii and Kistchinskii, 1972; Lentfer, 1975, 1976*a*; Stirling et al., 1975, 1977, 1978; Lentfer and Hensel, in press). Areas of den concentrations are reported from Wrangel Island, Franz Josef Land (Uspenskii and Chernyavskii, 1965; Uspenskii, 1977), Svalbard (Larsen, 1972, 1976), and southwest of Cape Churchill (Jonkel et al., 1972; Stirling et al., 1977). In Alaska, along the western edge of Banks Island, and throughout most of the Canadian High Arctic, dens are thought to be evenly distributed along the coast (Stirling et al., 1975, 1978; Lentfer, 1976*a*;

Lentfer and Hensel, in press). Maternity dens are often dug on slopes of 20 to 40° where snow has accumulated to depths of 1 to 3 m (Uspenskii, 1977). These dens are usually located within 8 km of the coast (Harington, 1968; Lentfer, 1976*a*; Lentfer and Hensel, in press; Uspenskii, 1977), and rarely beyond 48 km. Polar bears have been reported to bear young in maternity dens along the pack ice (Lentfer, 1975). Dens range from single chambers with short tunnels to complex structures with several chambers and tunnels (for detailed descriptions of maternity dens consult Uspenskii and Chernyavskii, 1965; Harington, 1968; Jonkel et al., 1972; Uspenskii and Kistchinskii, 1972; Lentfer, 1976*a*). Another type of den is a temporary shelter formed in the snow, particularly by females with young, during inclement weather (Jonkel et al., 1972; Lentfer, 1976*a*). A third type of den is dug into the earth, as a temporary shelter in summer and fall (Kolenosky and Stanfield, 1966; Doutt, 1967; Jonkel et al., 1972, 1976).

GENETICS. Crosses between brown bears and polar bears produced fertile hybrids (Gray, 1972). The 2n chromosome number is 74 (Low et al., 1964).

REMARKS. The first description and name of the polar bear, *Ursus maritimus*, means maritime bear. The reduction of stocks in the Soviet Union (Uspenskii, 1977) with subsequent moratoria on the taking of polar bears in the Soviet Union, Norway and the U.S. was interpreted by the news media to mean that polar bear numbers over their entire range were reduced. There is no evidence from studies in Alaska, Canada, or Greenland to support this opinion. No information is currently available on hereditary or genetic differences between the various sub-populations of polar bears.

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LARGE-SCALE SEA-SURFACE TEMPERATURE ANOMALIES IN THE NORTHEAST PACIFIC OCEAN

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ABSTRACT

Slow-developing, long-lasting perturbations of sea-surface temperature in the eastern North Pacific are revealed by anomaly patterns representing monthly deviations from the mean seasonal cycle. These patterns are typically defined by a central core of anomalously warm (or cold) water located approximately between latitudes 30°–45°N, and west of longitude 140°W, which is partially surrounded by anomalously cold (or warm) water to the north, east, and south. They can persist up to several years and then, in a relatively short time, undergo a pattern reversal in which warm anomalies are replaced by cold anomalies and vice versa. Some examples are presented that represent selected periods in the 1960s and 1970s. A comparison of mean wind fields for January 1976 and January 1980, which were periods of sharply contrasting sea-temperature anomaly patterns, suggest that air-sea interaction processes have an active role in forming and maintaining these patterns.

RESUMEN

Perturbaciones de lento desarrollo y larga duración de temperaturas de la superficie del mar en el Pacífico nordeste son reveladas por patrones de anomalías que representan desviaciones mensuales del ciclo estacional medio. Estos patrones se identifican típicamente por un núcleo central de agua anómalamente templada (o fría), que se encuentra aproximadamente entre las latitudes 30° y 45°N, y al oeste de la longitud 140°O, y que está parcialmente rodeado por agua anómalamente fría (o templada) al norte, este y sur. Los patrones pueden persistir durante unos cuantos años y de repente, en un período relativamente corto, se puede reversar el patrón, donde se reemplazan las anomalías templadas con anomalías frías y viceversa. Se presentan algunos ejemplos que representan períodos selectos durante los 1960s y los 1970s. Una comparación del promedio de los campos del viento para enero de 1976 y enero de 1980, períodos en que se exhibían patrones anómalos contrastantes de temperatura marina, sugiere que los procesos de interacción aire-mar juegan un papel activo en la formación y el mantenimiento de estos patrones.

INTRODUCTION

Large-scale departures of sea-surface temperature from mean conditions in the North Pacific Ocean can persist over extensive periods of time. Surface temperatures reflect thermal conditions in the entire upper mixed layer, which may reach to depths of 100m or more. Consequently, a variation of 1° or 2°C from normal may reflect a significant gain or loss of heat in this layer.

Monthly charts of sea-surface temperature for the northeast Pacific, along with charts showing deviations from long-term monthly means, have been prepared since 1960 for Fishing Information (Southwest Fisheries Center). These charts are based on data contained in radio reports of ship's synoptic weather observations, collected through the National Weather Service. The sea-surface temperature fields were analyzed from values averaged for areas 1° latitude by 1° longitude. Anomaly charts were constructed by subtracting the corresponding long-term monthly mean field from the analyzed termperature field for a particular month. Prior to 1974, the long-term monthly means were based on charts in H.O. 225 (U.S. Hydrographic Office). After that, a new set of monthly means were prepared from data representing the period 1948–67, obtained through the U.S. Navy's Fleet Numerical Weather Facility. All of the figures presented here were taken directly from, or are based on, charts published in Fishing Information. Temperature units used for these charts were converted from Fahrenheit to Celsius between 1977 and 1978. Consequently, both kinds of units appear in the figures.

The charts are all based on observations from January so that interyear comparison will be unaffected by seasonal variation and because sea-surface temperatures in winter months are less affected by transient fluctuations in thin surface layers.

SEA-TEMPERATURE ANOMALY PATTERNS

The examples selected for presentation here depict anomaly patterns that are typically defined by a central core of anomalously warm (or cold) water located approximately between latitudes 30 °–45 °N, and west of longitude 140 °W, which may be partially surrounded by anomalously cold (or warm) water to the

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north, east, and south. Similar patterns have been found for periods in the 1950s (Eber 1971).

Figure 1 shows the sea-temperature anomalies for January 1965 and represents a regime characterized by positive values in the central core with scattered areas of negative anomalies in the peripheral region. This was a very stable pattern which persisted more than three years, into 1968. Figures 2–4 show the evolution of this regime in successive Januarys. The warm central core remained the dominant feature throughout the period, in terms of both spatial distribution and magnitude of deviations from normal conditions. In January 1967 the negative anomalies had nearly vanished, but by January 1968 the pattern had returned to a state remarkably like that of January 1965.

This general type of regime characterized by a warm central core and cool periphery reappeared again in January 1974 (Figure 5). However, in this case the negative anomalies were the dominant feature, extending well offshore along the entire west coast of North America. At this time, the central core of the positive anomalies was poorly defined. During the ensuing year, however, the evolution of the warm core continued between latitudes 25°–35°N while the negative anomalies spread further into the surrounding areas, as shown in Figure 6. By January 1976 (Figure 7) the warm central core had consolidated in the vicinity of latitude 30°N, longitude 160°W and was almost completely encircled by the peripheral cold region.

In 1976, a transition began to take place which led to a nearly complete pattern reversal in the anomaly field. Figure 8 depicts the new regime as it existed in January 1977, with a central cold core between latitudes 35°–40°N and relatively warm conditions everywhere east of longitude 145°W. During 1977, the negative anomalies spread eastward to about longitude 135°W while positive anomalies spread out along the southern periphery (Figure 9). Midway through 1978, a disruption of the pattern occurred, which led to the occurrence of negative anomalies along the coastal zone and in most of the area between latitudes 25°–35°N (Figure 10). This was relatively short-lived, and by January 1980 the typical pattern characteristics were again evident (Figure 11).

Although it is beyond the scope of this paper to try to explain why these patterns of anomalous sea-temperature distributions develop, it is reasonable to assume that air-sea interaction processes are involved. In particular, one would expect to find contrasting atmospheric conditions corresponding to contrasting sea-temperature anomaly patterns. The anomaly fields for January 1976 and January 1980 are examples of opposite temperature regimes (Figures 7 and 11). Figure 12 shows the difference in the temperature fields for these two months. These differences portray an enhanced image of the typical anomaly pattern described in this study. Negative differences in the central core area represent lower temperatures in 1980 than in 1976, and positive differences along the North American coast and in the peripheral region represent higher temperatures in 1980 relative to 1976.

For comparison, Figure 13 shows the difference in the surface wind field for January 1976 and January 1980. The arrows represent the vector difference of wind observations averaged by areas 5° latitude by 5° longitude for the respective months. In terms of air circulation, Figure 13 shows that the flow in 1980 was from the south (relative to that in 1976), east of longitude 135°W and south of latitude 40°N, where the maximum positive temperature differences occurred. Conversely, the flow in 1980 was from the north (relative to that in 1976) in the area between latitudes 25°–35°N and longitudes 145°–160°W, where the maximum negative temperature differences occurred.

The magnitude of differences in wind speed between the two years is substantial, and the described relationships between differences in winds and sea temperatures are consistant with the effects that would be expected from wind-induced advection, evaporation, and sensible heat transfer. It appears likely, therefore, that air-sea interaction processes have a tangible role in forming and maintaining persistant patterns of sea-surface temperature anomalies.

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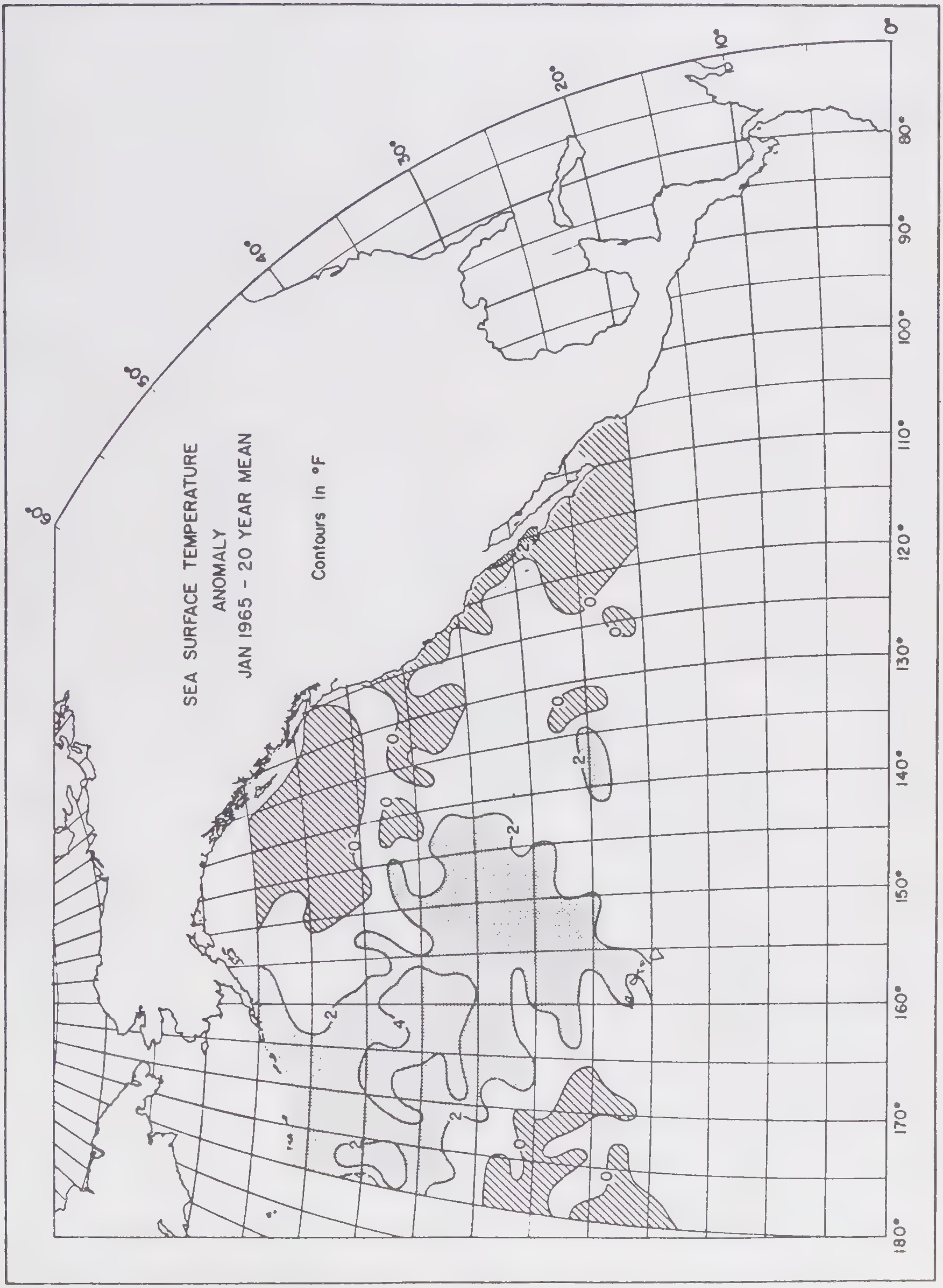

Figure 1. Deviation of sea-surface temperature for January 1-31, 1965, from the long-term mean. Hatched areas colder in 1965, clear and stippled areas warmer in 1965.

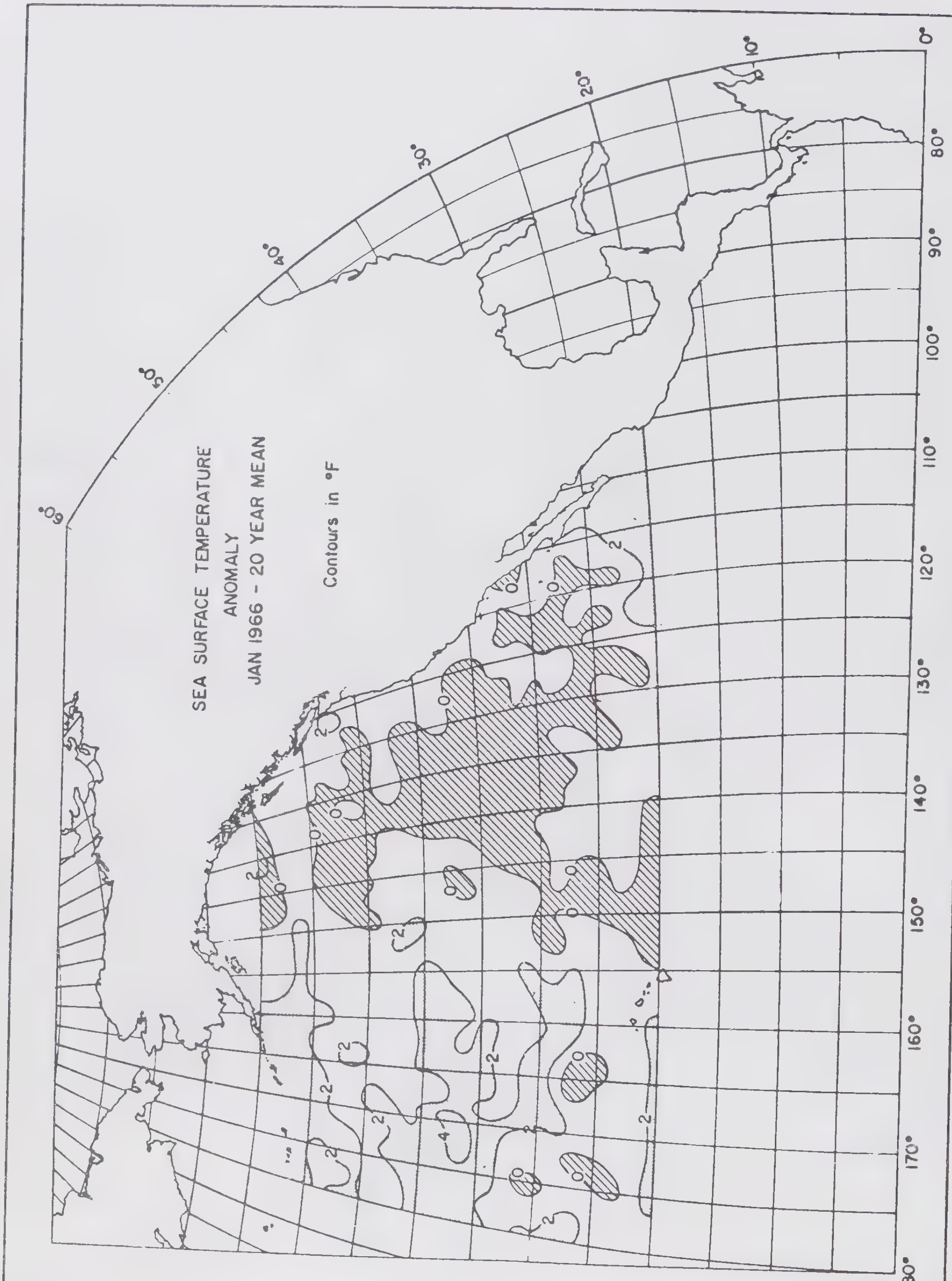

Figure 2. Deviation of sea-surface temperature for January 1-31, 1966, from the long-term mean. Hatched areas colder in 1966, clear and stippled areas warmer in 1966.

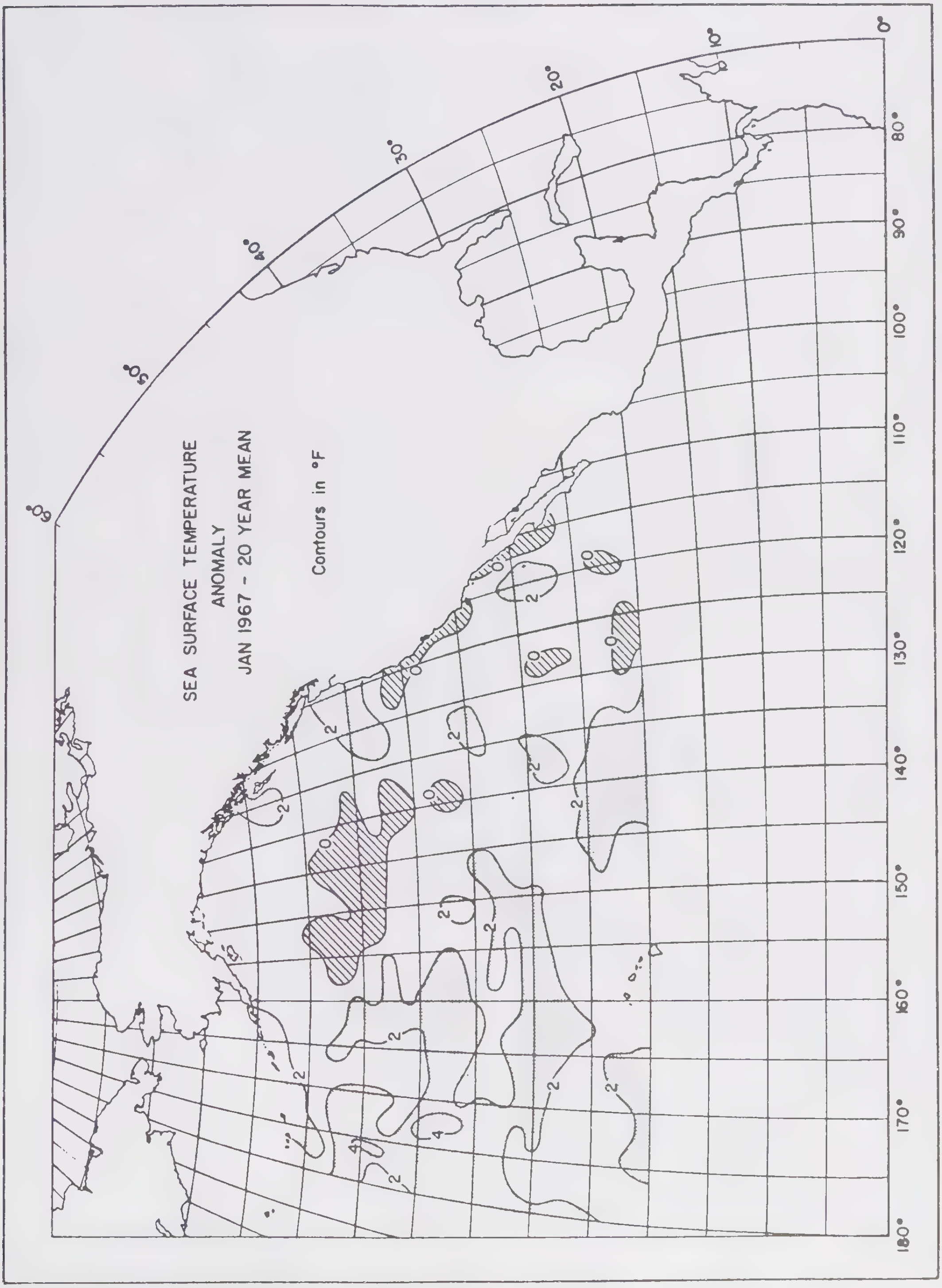

Figure 3. Deviation of sea-surface temperature for January 1-31, 1967, from the long-term mean. Hatched areas colder in 1967, clear and stippled areas warmer in 1967.

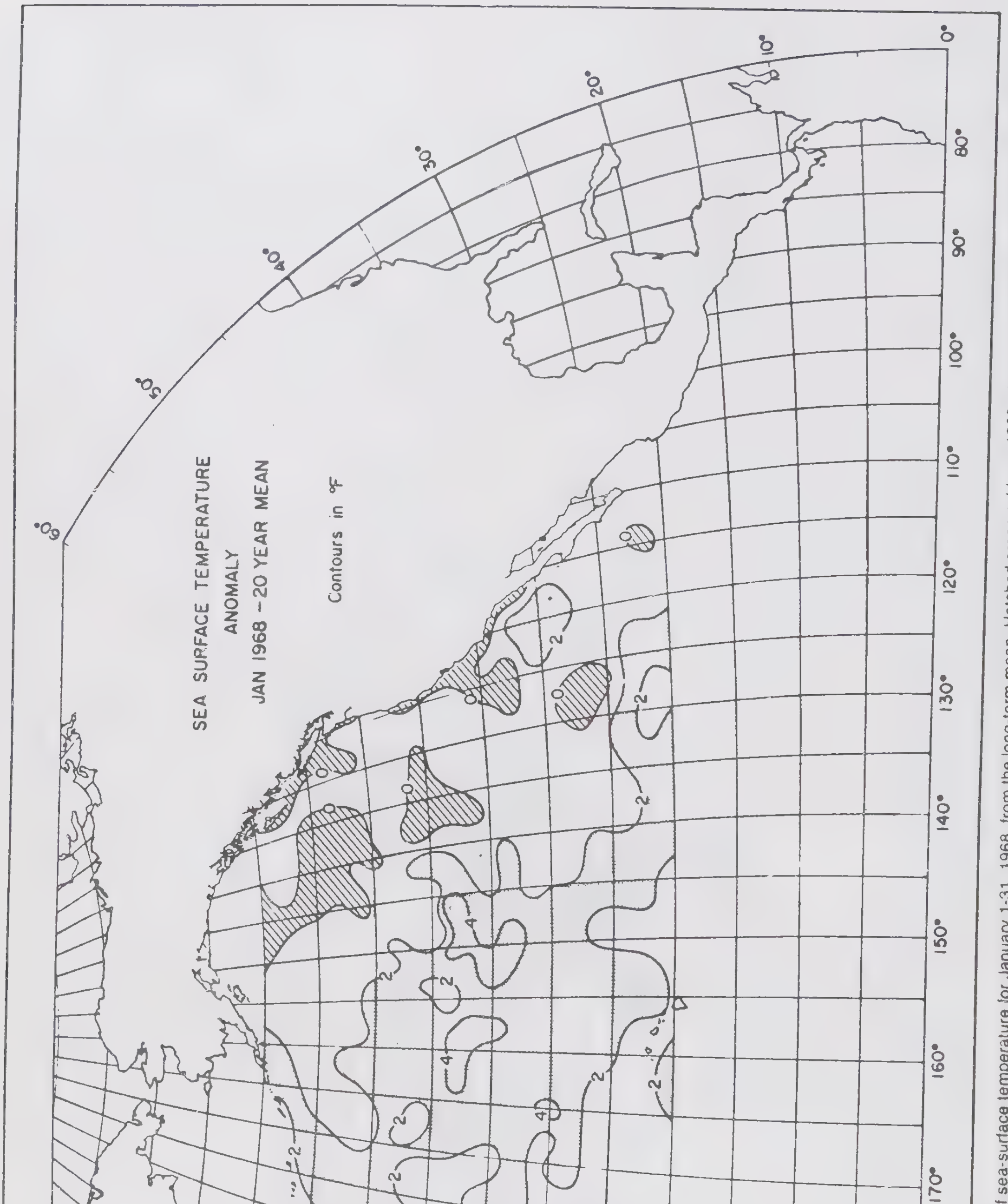

Figure 4. Deviation of sea-surface temperature for January 1-31, 1968, from the long-term mean. Hatched areas colder in 1968, clear and stippled areas warmer in 1968.

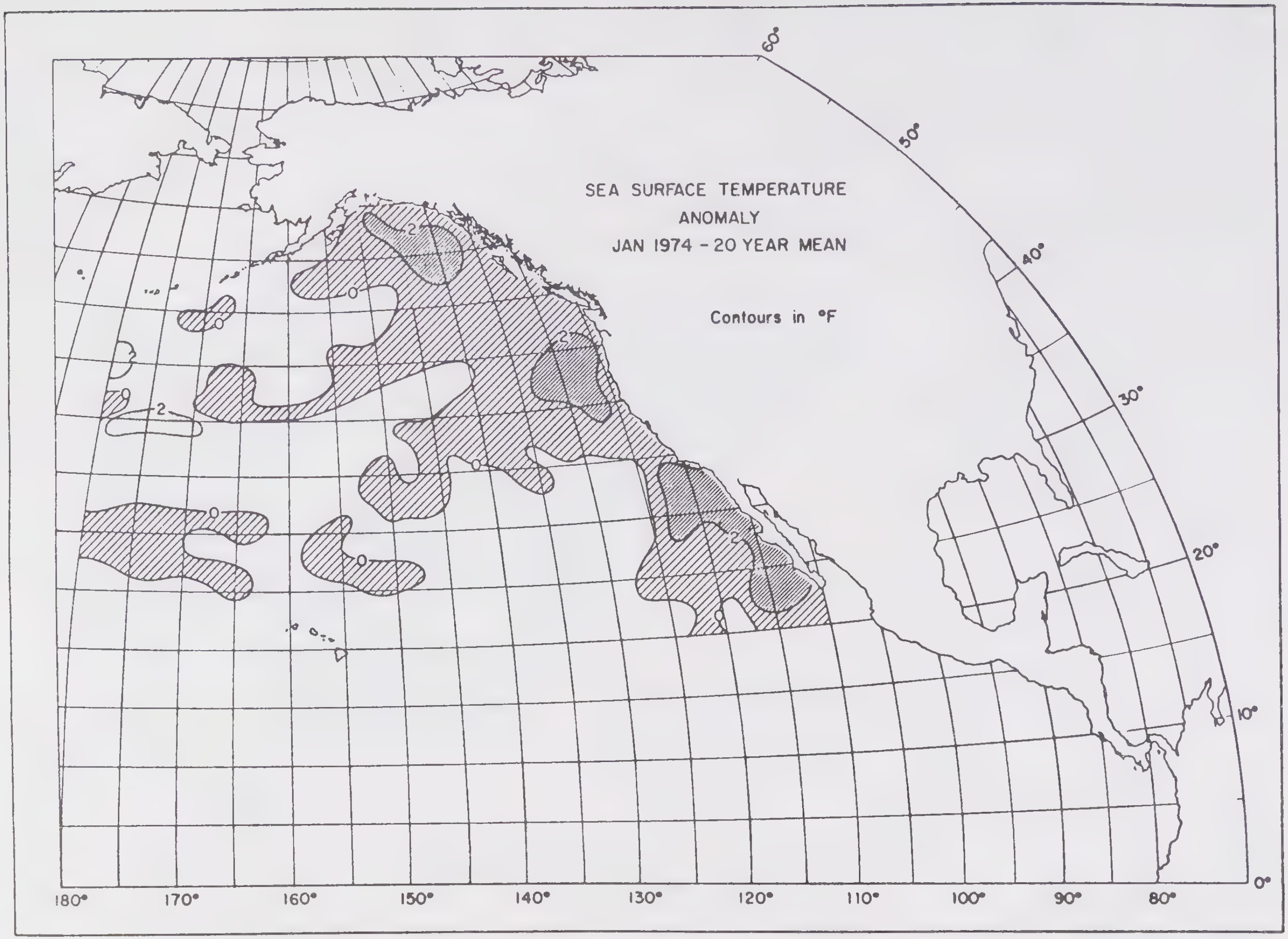

Figure 5 Deviation of sea-surface temperature for January 1-31, 1974, from the long-term mean. Hatched areas colder in 1974, clear and stippled areas warmer in 1974.

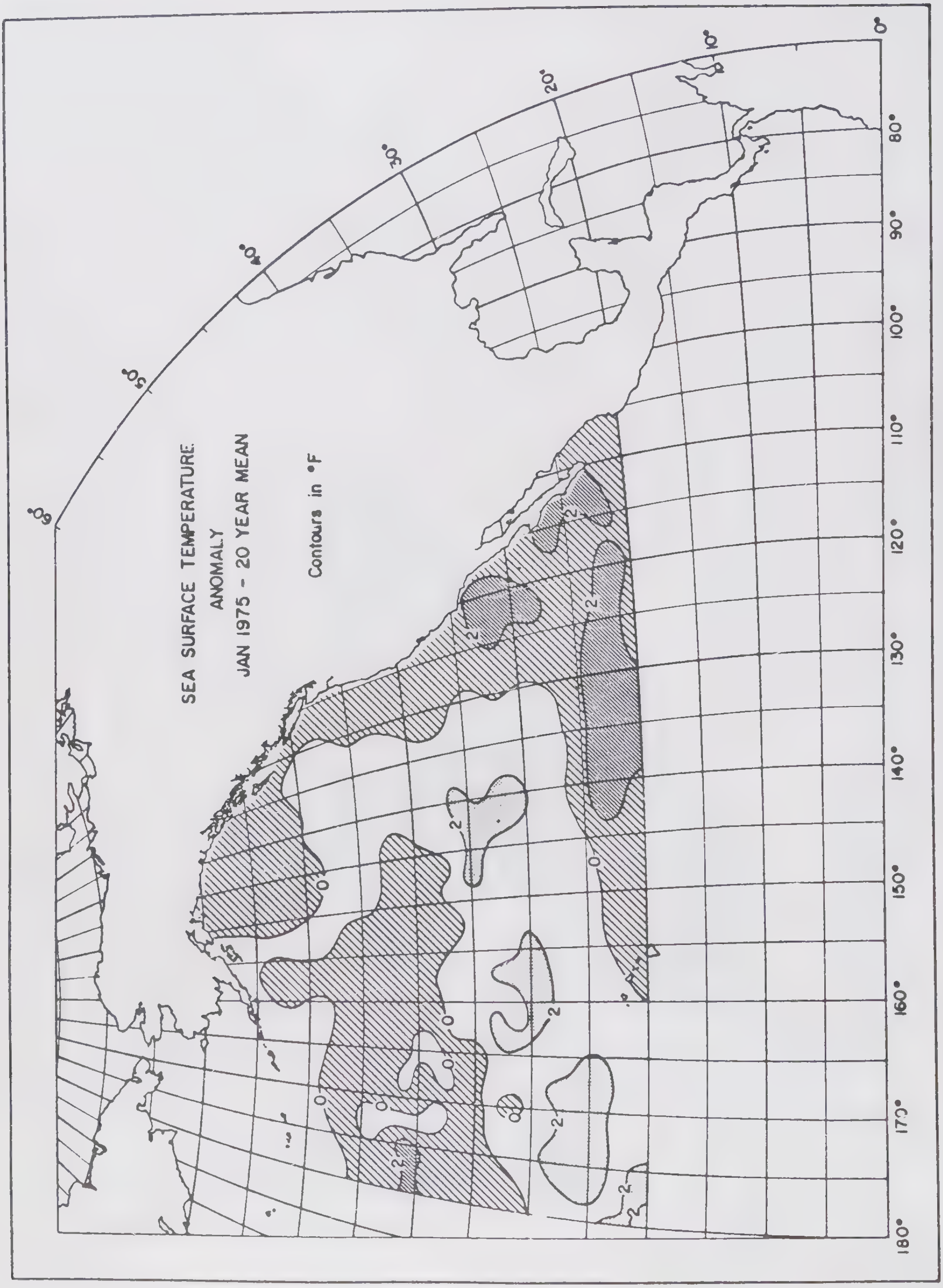

Figure 6. Deviation of sea-surface temperature for January 1-31, 1975, from the long-term mean. Hatched areas colder in 1975, clear and stippled areas warmer in 1975.

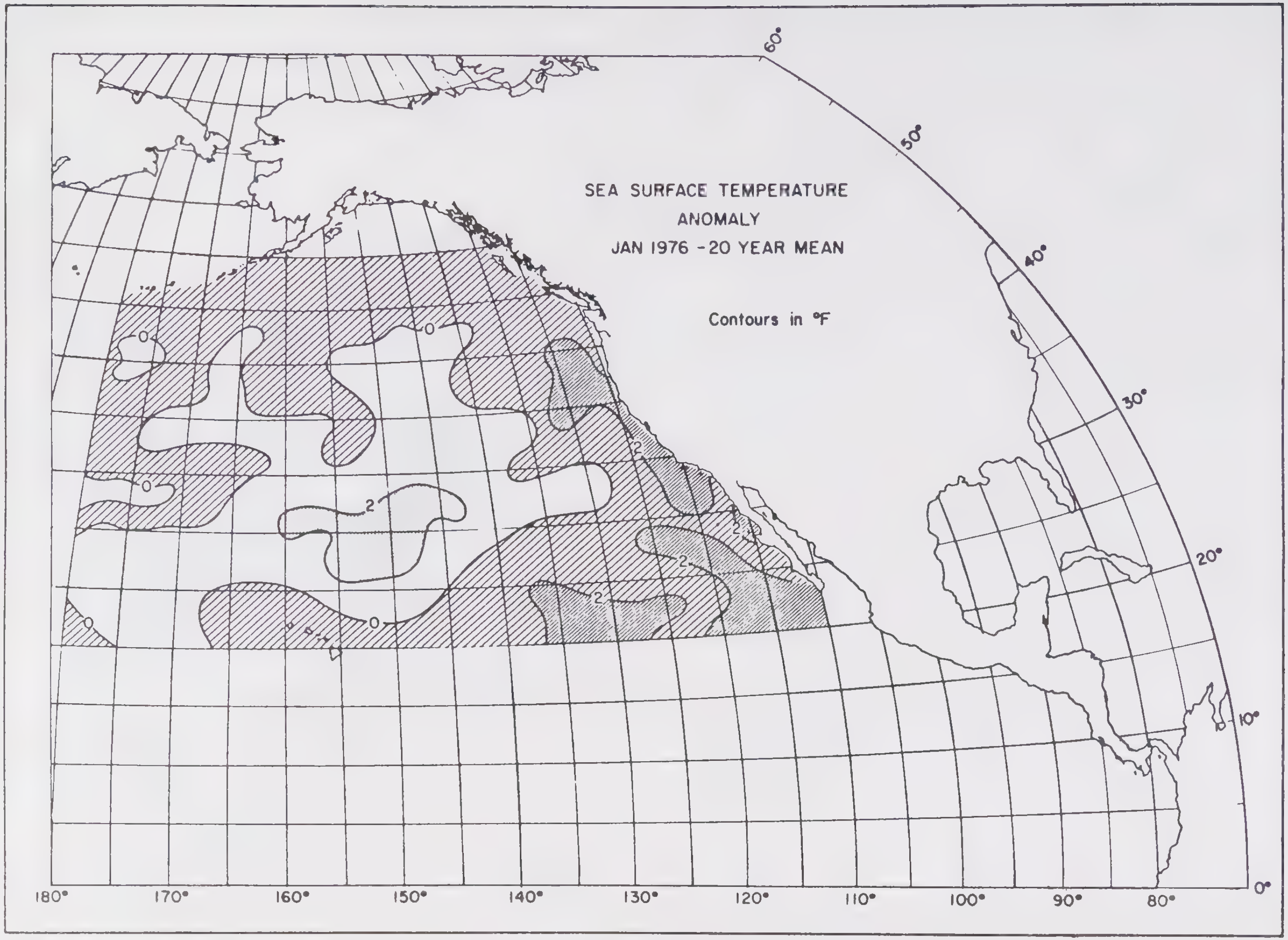

Figure 7. Deviation of sea-surface temperature for January 1-31, 1976, from the long-term mean. Hatched areas colder in 1976, clear and stippled areas warmer in 1976.

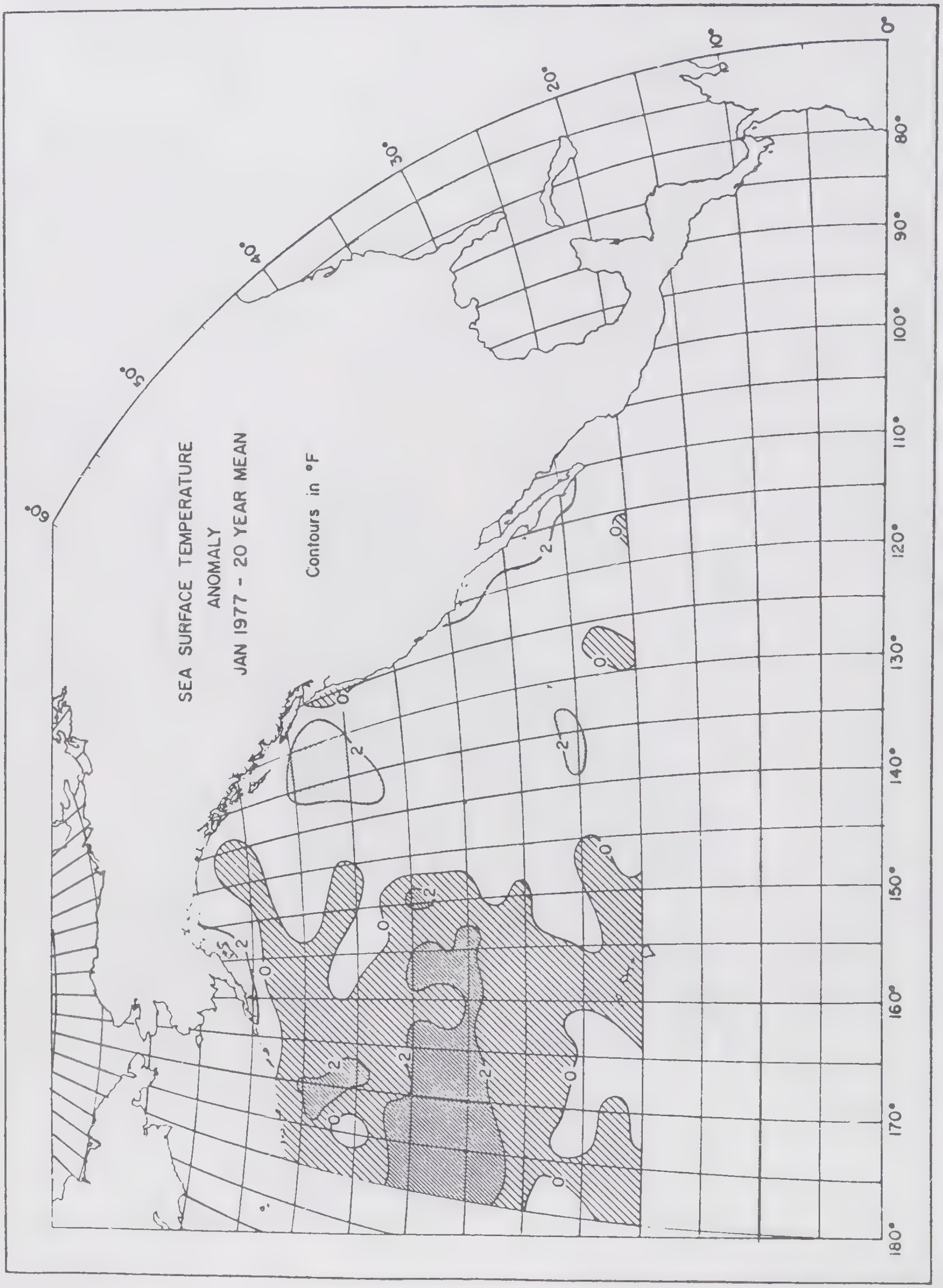

Figure 8. Deviation of sea-surface temperature for January 1-31, 1977, from the long-term mean. Hatched areas colder in 1977, clear and stippled areas warmer in 1977.

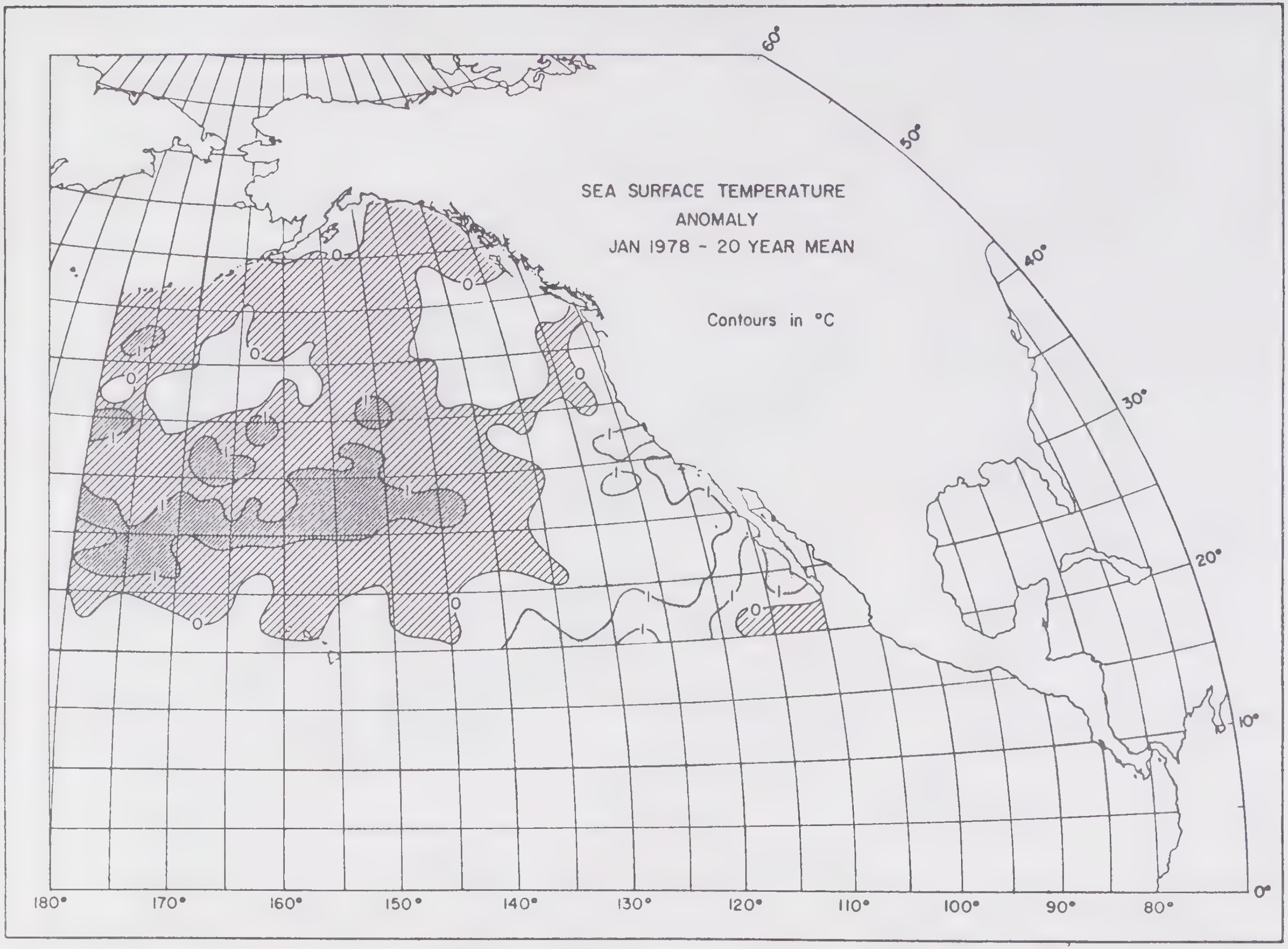

Figure 9. Deviation of sea-surface temperature for January 1-31, 1978, from the long-term mean. Hatched areas colder in 1978, clear and stippled areas warmer in 1978.

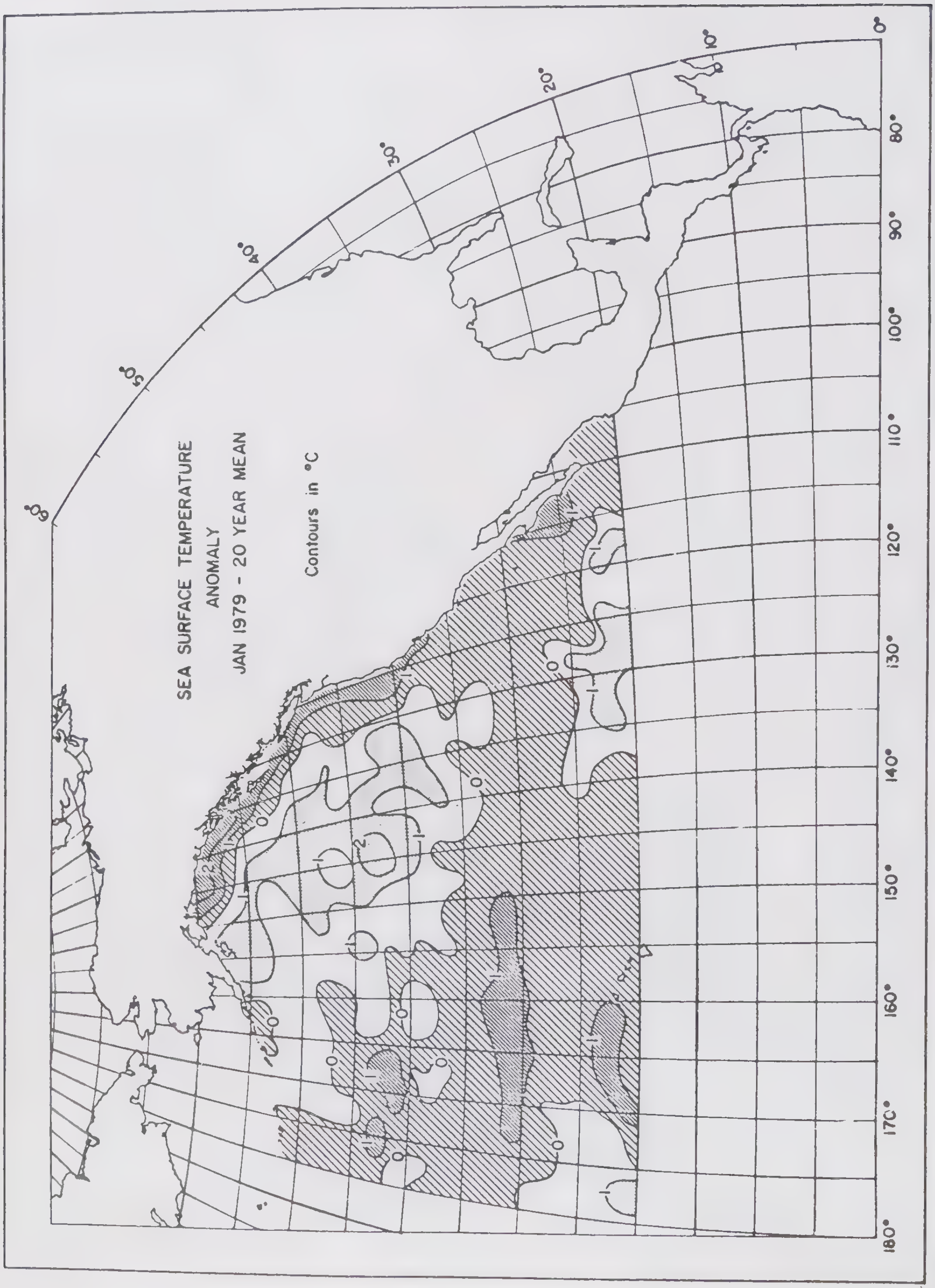

Figure 10. Deviation of sea-surface temperature for January 1-31, 1979, from the long-term mean. Hatched areas colder in 1979, clear and stippled areas warmer in 1979.

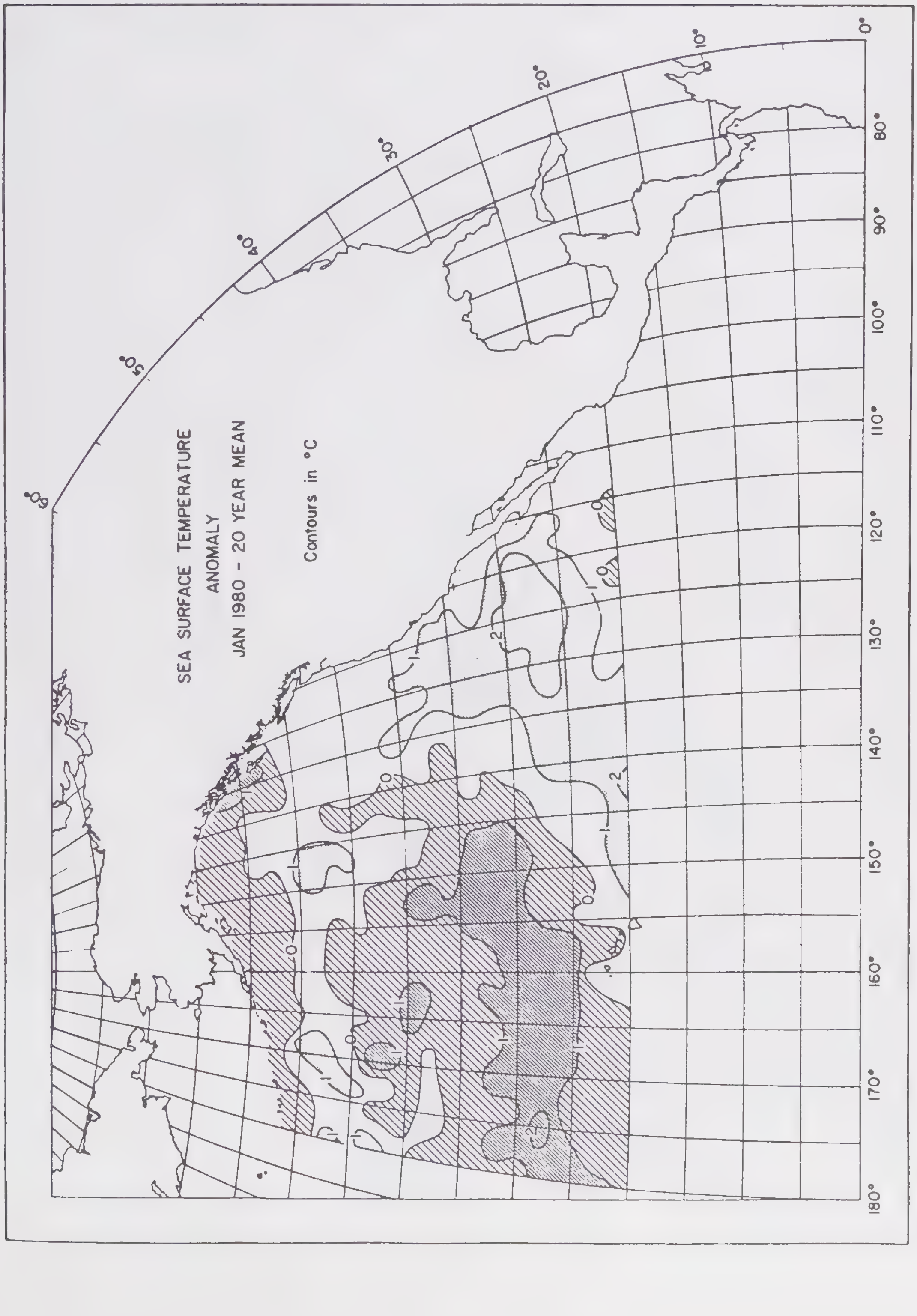

Figure 11. Deviation of sea-surface temperature for January 1-31, 1980, from the long-term mean. Hatched areas colder in 1980, clear and stippled areas warmer in 1980.

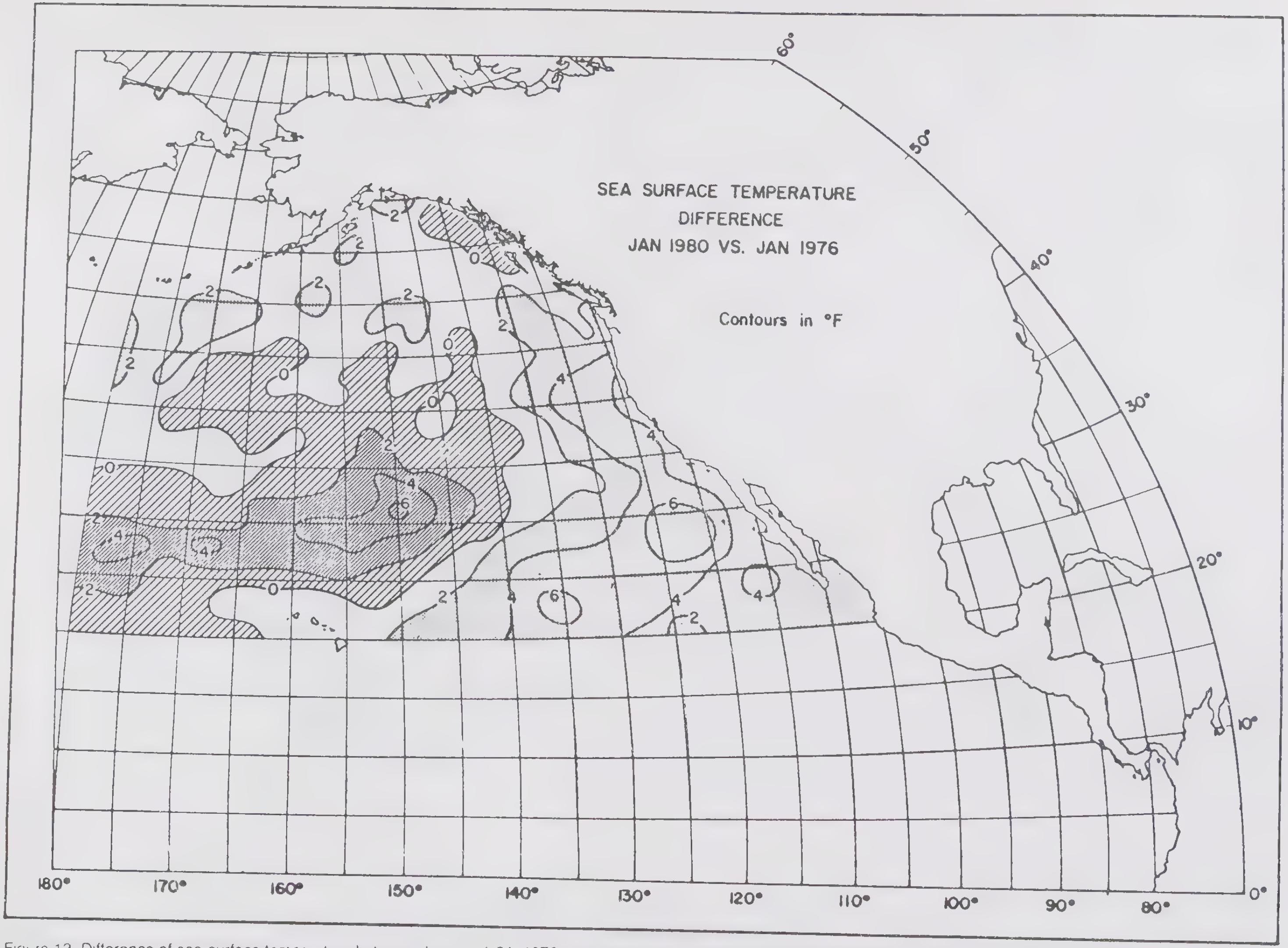

Figure 12. Difference of sea-surface temperature between January 1-31, 1976, and January 1-31, 1980. Hatched areas colder in 1980, clear and stippled areas warmer in 1980.

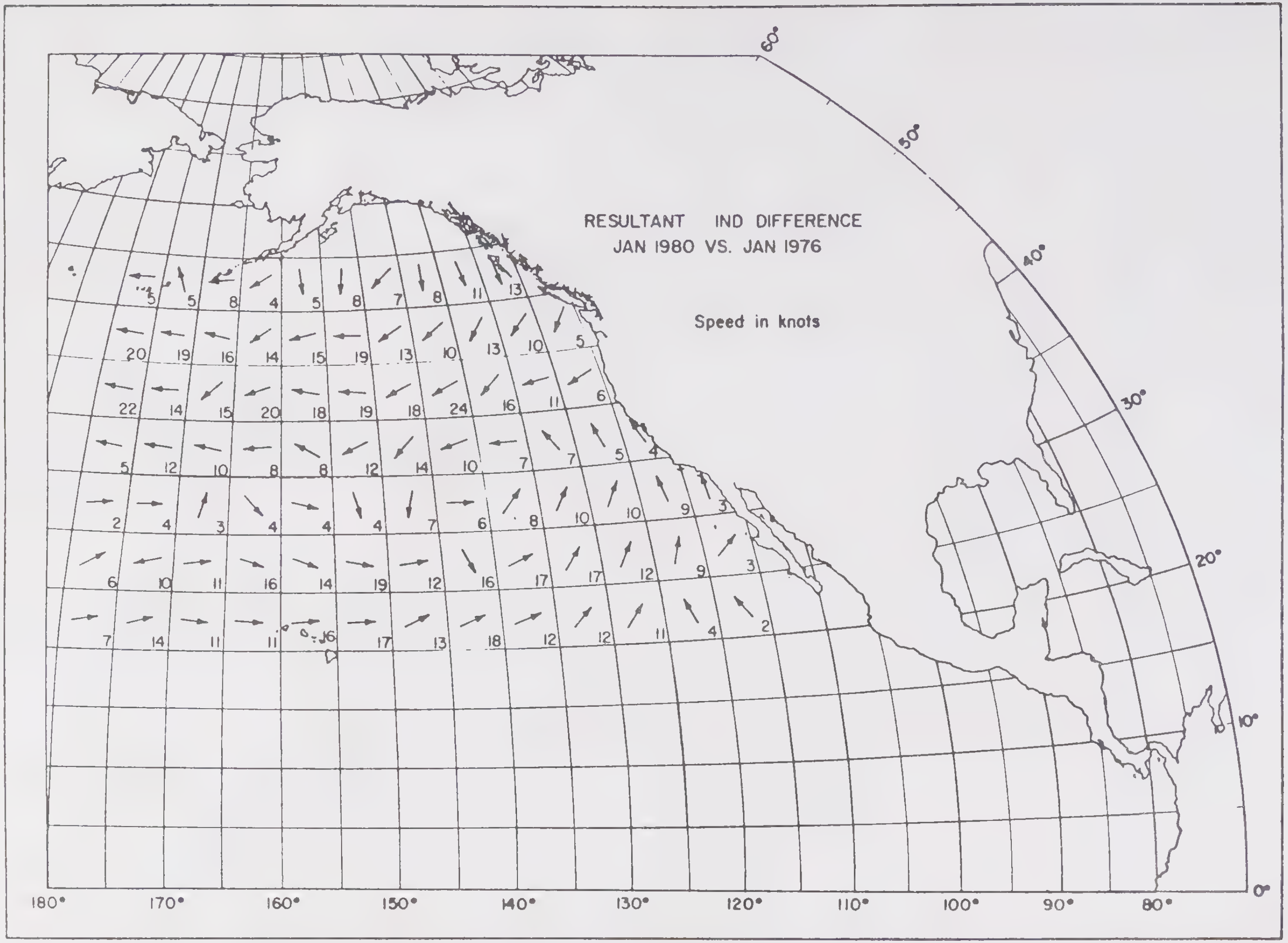

Figure 13. Arrows represent vector differences of winds averaged by areas 5° latitude by 5° longitude for January 1-31, 1976, and January 1-31, 1980. Numbers represent corresponding differences in wind speed. Differences were computed by subtracting 1976 from 1980 values.

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ENDOGENOUS ENERGY SOURCES AS FACTORS AFFECTING MORTALITY AND DEVELOPMENT IN STRIPED BASS (*MORONE SAXATILIS*) EGGS AND LARVAE

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Since its introduction in 1879 the striped bass population in the San Francisco Bay-Delta estuary has fluctuated in abundance. During the last nine years the population has steadily declined causing concern among resource managers, scientists and citizens. Extensive field studies with 15 years of data available have found that variation in striped bass abundance relates directly to survival in the first 60 days of life (Chadwick et al., 1977; Chadwick, 1979). These studies, however, have not been able to determine the direct or primary causes of early life stage mortality. Current hypotheses contend that factors associated with freshwater outflow in the two major rivers and diversion of river water to the California aqueduct system directly affect striped bass eggs and larvae by physical removal or nursery habitat alteration. Four years ago we began laboratory studies on factors affecting egg and larval mortality (Eldridge et al., in press). Emphasis was placed on those factors associated with larval food and feeding. In the course of these studies we soon discovered the endogenous energy sources played critical roles in the survival, growth and differentiation of the embryos and early larvae.

A series of seven complete experiments were conducted closely examining daily survival, growth (tissue dry weight and standard length), differentiation (tissue histology, ossification, general organogenesis), and bioenergetics in relation to different live food rations. In conjunction with these laboratory experiments spawning adults were collected from the field and extensively autopsied to determine the extent parental conditions affected gametic viability and quality. Special attention was given to the ovarian eggs of these field specimens and the components which comprised the endogenous energy sources of the embryos and larvae.

Striped bass spawn pelagic eggs which become large (average diameter = 3.40 mm for Atlantic fish, Mansueti, 1958; 3.28 mm for Pacific fish, Meinz and Heubach, 1977) with a wide perivitelline space in which the embryo — yolk — oil complex floats. Prior to water hardening we found our eggs to average 1.03 mm in diameter. Eggs contain two energy sources — yolk and oil, the latter contained in a single, spherical oil globule. Chemical analysis showed that yolk was comprised mostly of proteinaceous material with an average lipid content of 3.8%. The oil globule makes up over half of the total dry weight and most of the energy of the egg (Table 1). Fatty acid scans of the oil globules showed no significant differences in the fatty acid compositions of oil globules in eggs from three different females. More definitive chemical analyses are planned to determine whether this homogeneous condition extends to all the lipid components of the oil globule. On a quantitative basis close examination of eggs from 34 spawning striped bass showed large differences in the proportions of yolk and oil to total egg dry weights, and differences in the amounts of yolk and oil in eggs from different females. Dry weights of yolk ranged 28 to 81% of the total egg dry weights. The coefficient of variation for the yolk weights was 20%. Oil contents ranged 12 to 67% with a c.v. of 19%. The average amounts of yolk and oil found in the eggs is given in Table 1. The ranges of weights extended from 41 to 226 μg for yolk and 34 to 251 μg for oil. Causes for these variations are still under study. Preliminary results suggest age, parental condition, genetic

Table 1. Dry weights, caloric, lipid, water and ash contents of eggs from 34 field-caught striped bass in spawning condition.

	Dry weight (μg)	Caloric content (Calories/g)	Lipid content (% of dry wt.)	H_2O content (% of wet wt.)	Ash content (% of dry wt.)
Yolk					
$\overline{X}$	104.0	5 657	3.8	53.7	3.0
S.D.	27.8	38	1.5	3.3	0.5
Oil					
$\overline{X}$	112.3	9 492	100.0	0.0	0.0
S.D.	27.9	297	—	—	—
Total Egg					
$\overline{X}$	232.3	7 803	52.0	53.7	3.0
S.D.	58.6	392	5.7	3.3	0.5

relation, pollutant load, and time are primary factors.

As embryonic and larval development proceeded yolk energy was consumed first. Total yolk absorption approximately coincided with the onset of feeding. Yolk utilization rates did not significantly differ. An average 62% of the original oil energy remained in the larvae at the time of initial feeding, seven days after fertilization. The rates at which this remaining oil energy was utilized directly depended on food availability. The larger the food ration the faster was oil consumed. At 18°C larvae feeding at a ration of 48.05×10^{-5} calories/ml consumed their oil energy within an average 19–21 days while starved larvae conserved their oil energy until death, as long as 29–34 days after fertilization.

Larvae with higher daily food rations and faster oil energy consumption rates survived at significantly higher rates than starved and low ration larvae. Starved larvae also exhibited no point-of-no-return (Eldridge et al., in press). Larvae which survived to the time of food introduction underwent an initial adjustment to feeding. They then continued to survive and develop similar to larvae which began feeding at a normal age.

Sizes of embryos and larvae correlated with the initial egg size, that is, the original amount of endogenous energy. This was reflected in the significant differences between the elevations of the growth curves of embryos and larvae from different females. Further differences, though less significant, were seen in the growth rates or slopes of offspring from different fish.

This complexity of growth suggested to us that some parental factor or condition could possibly be active and led us to examine parental tissues for pollutants. Preliminary chemical analyses showed that the eggs of field-caught spawning fish contained potentially toxic pollutants (Table 2). The presence of heavy metals and hydrocarbons can affect the mobilization of energy resources within the female as they are deposited in the egg resulting in reduced fecundity and/or smaller eggs. These pollutants can also affect later growth and survival of embryos and larvae as the toxicants are slowly released with the utilization of the yolk and oil. Experiments are currently underway to study the extent of these effects.

Table 2. Concentrations of heavy metal and hydrocarbon pollutants found in eggs of California striped bass.

	Heavy metals (μg/g; wet weight) n = 46			Cyclohexanes and aromatic hydrocarbons (μg/g; wet weight) n = 20
	Zinc	Iron	Copper	
Mean	26.7	11.7	3.2	0.053
Range	19.1–86.6	[a]0–19.5	[a]0–7.4	[a]0–0.426

[a] Concentrations were below the level of detectability of our procedure.

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Physiologic Responses of Striped Bass (*Morone saxatilis*) Embryos and Larvae to Low, Sublethal Concentrations of the Aromatic Hydrocarbon Benzene

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RESUMEN

El "striped bass" es un pez de importancia deportiva y comercial y que pasa toda su vida en estuarios y aguas costeras. Dado que es un predador final en la cadena alimenticia y emplea los estuarios para desove y desarrollo de la cría, es un buen indicador de las condiciones saludables del biota estuarino. Recientemente, encontramos hembras cargadas en el Delta estuario de la Bahía de San Francisco, en los Estados Unidos, que estaban contaminados con una variedad de contaminantes, los que incluía la benzina hidrocarbónica aromática, derivada del petróleo. Por lo tanto, los experimentos de laboratorio fueron ensayos para probar los efectos que baja concentración, concentraciones subletales (promedio 159 a 248 ppb) de C^{14} rotulados benzina, podían tener en el "striped bass" desde la fecundación a la metamórfosis.

Todas las fases vitales (o evolutivas) absorbienron benzina rápidamente, casi siempre en cuestión de horas, y concentraban los hidrocarburos a niveles mayores que las concentraciones acuosas presentes. Las larvas más desarrolladas, en su alimentación, concentraban la mayor parte de los hidrocarburos, demostrando que la benzina se acumula en los tejidos, tanto por la vía alimenticia como la acuática.

La benzina provocaba desoves anticipados y niveles más altos de sobrevivencia, pero estos beneficios aparentes eran anulados por la mortandad latente después de la contaminación. Larvas prealimentadas y expuestas a la benzina sobrevivían, y no se encontró diferencias en larvas más desarrolladas. Larvas avanzadas y hambrientas sufrieron mayor esfuerzo, muriendo más rápidamente que las no expuestas.

El metabolismo de los embriones y larvas expuestas fué consistentemente más intenso que en los controles, pero ello no se reflejaba en las comparaciones de crecimiento. Al contrario, las larvas expuestas crecian a un ritmo mas rapido que los controles después del período de exposición.

Estos resultados se analizan, dado que se relacionan a vías y efectos conocidos de otros hidrocarburos derivados del petróleo. Se presentan las consecuencias de estos efectos según se manifiestan a nivel de población.

INTRODUCTION

Lay and scientific communities are becoming increasingly more aware and outspoken about the ubiquity of toxic substance (White, 1980; Magnuson, 1980). A large portion of the toxicants found in the aquatic environment originate from petroleum. In fact, most of the Environmental Protection Agency's list of priority pollutants contain compounds which are derived from or are mixed with petrochemicals. Monocyclic aromatic hydrocarbons are generally considered one of the most toxic of the petrochemicals and benzene is the simplest and most basic structure common to all aromatic hydrocarbons. Benzene is found in crude oil and refined products. It is relatively water soluble and has a log partition coefficient of 2.80, meaning it tends to concentrate in fatty tissues.

A small but increasing data base of field measurements show concentrations of benzene in open ocean waters range approximately 0.01 to 5.00 ppb ($nl l^{-1}$) (Whipple et al., 1980a). Nearshore and estuarine waters contain benzene at 1 to 100 ppb and up to 200 ppb in fresh waters. These levels represent residual levels from chronic inputs, whereas petrochemical spills cause higher concentrations. For example, water samples collected around the crude oil plume of the recent IXTOC wellhead spill contained 60 to 100 ppb of benzene. Concentrations decreased with distance from the plume to open ocean residual levels of approximately 1 ppb (Payne et al., 1980).

Studies conducted at our laboratory on the commercially and ecologically important striped bass (*Morone saxatilis*) showed fish tissues (mainly liver and ovary) contained relatively high concentrations of benzene (Whipple, 1979; 1980; Whipple et al., 1980b; Jung and Bowes, 1980). The amounts found suggest the adult fish are being exposed to low level chronic concentrations in the wild. These conclusions are based on our own experience in the laboratory with exposures of adults to benzene.

Striped bass is an anadromous fish found in coastal waters of East, West and Gulf states of the United States. It is a terminal predator in the food chain and spawns large pelagic eggs. Larvae characteristically use shallow, often industralized, estuaries as nursery grounds. Juveniles and adults range into marine environments and sometimes migrate long distances. Unfortunately populations in the northeastern and western United States are experiencing unprecedented declines. Egg viability and survival of early life stages also seem affected (personal communication, Robert Stevens, U.S. Fish and Wildlife Service, Washington, D.C.; Donald H. Stevens, California Department of Fish and Game, Stockton, California).

Pollution is one of the causal factors most implicated in the population declines. Because benzene was present in adult fish it appears likely younger stages might also be exposed to the chemical. We therefore designed a series of experiments (a) to determine amounts and rates the early life stages take up when exposed to low level, sublethal concentrations, and (b) to measure as comprehensively as possible how these accumulated hydrocarbons affect the physiology of these organisms.

MATERIALS AND METHODS

Early life stages of striped bass are easily divided on a physiological and developmental basis into three stages: embryo, from fertilization to hatching (Day-0 to Day-2); prefeeding larva, from hatching to first, exogenous feeding (D-2 to D-7); and feeding (and starved) larva, from the time when feeding normally begins to metamorphosis (D-7 to D-29). The different aspects of this study are organized around these three life phases with benzene exposure occurring within each phase and measurements taken during and after the completion of the particular life stage. The purpose of this strategy was to determine how individuals within a given life stage respond to benzene and to see if latent effects occurred after exposure.

Sexually mature electrofished adults from the Sacramento River, California, were injected with gonadotropins and artificially spawned. Eggs were incubated in flow-through McDonald jars. Newly hatched prefeeding larvae were transferred to semispherical 8-L acrylic plastic rearing containers held in water tables for temperature stability. Animals were reared from hatching to metamorphosis in

Table 1. Experimental conditions of benzene exposure to striped bass and larvae

Life Stage	Type of Exposure	Exposure Duration (days)	Sample Type	Sampling Frequency (time after initial exposure)
Embryo	Continuous slow	0-2	water	0, 3, 6, 12, 24, 33, 42 h
			tissue	1, 3, 6, 12, 24, 36 h
Prefeeding Larvae	Semi-static	2-7	water	0, 1, 3, 6, 12, 24 h; daily thereafter.
			tissue	1, 3, 6, 12, 24 h; daily thereafter.
Feeding & Starved Larvae	Semi-static	8-24	water	0, 3, 6, 12, 24 h; daily thereafter.
			tissue	1, 3, 6, 12, 24 h; daily thereafter.

these containers. Initial stocking densities depended on the type of study being run — approximately 150 larvae in all but survival tests (those had 20 larvae per container). We attempted to duplicate natural water quality conditions as much as possible. Temperatures were held at 18.0 ± 0.5° C and oxygen contents were at or near saturation. Photoperiod and light qualities were controlled and close to natural. Salinities were zero from fertilization to D-4, 1.0 ppt from D-5 to D-13, and 3 ppt from D-14 to D-29. Containers were cleaned and new water and live food (newly hatched *Artemia salina* nauplii in densities of 5.0 nauplii ml^{-1}) added daily.

Animals were exposed to C^{14}-benzene in continuous flow and semi-static systems depending on the type of culture system (Table 1). Target benzene concentrations were 100 to 200 ppb throughout the experiment. Water and tissue samples were analyzed for benzene by gas chromatography (Hewlett Packard 5840) and standard radiometry (tissue digestion and counting on a Packard Tri Carb scintillation spectrometer).

Immediate mortality was measured during each exposure period and delayed mortality after exposure. Each group was monitored to D-29 or complete mortality. Embryonic mortality was determined from direct counts of dead eggs which had floated out of McDonald jars. Larval mortality was estimated by visual counts in test containers.

Growth was determined from subsamples of embryos and larvae that were measured for standard lengths (via ocular micrometer) and dissected apart to separate oil globule, yolk and assimilated tissue. Tissue samples were dried at 60° C for 24 h and weighed on a Cahn electrobalance.

Bioenergetic variables in this study and the methods used to measure them are similar to those of Laurence (1977) and Eldridge et al. (1977). The caloric contents of

Table 2. Summary of sampling frequencies and sizes in the study of the effects of benzene on striped bass embryos and larvae

Life Stage	Age (days)	C^{14} Uptake sf*	Survival sf*	Survival replicate size	Growth sf*	Growth sample size (n)	Bioenergetics sf*	Bioenergetics sample size (n)
Egg	0-2	varied (see Table 1)	every 12 h	2	every 12 h	20-30	every 12 h	30-50
Prefeeding Larvae	2-7	1st 24 h & daily	daily	4	daily	10-20	daily	10-20
Feeding & Starved Larvae	8-29	1st 24 h & daily	daily	4	alternate days	10-20	alternate days	10-20

*sf = sampling frequency

endogenous energy sources were obtained by careful dissection and weighing of egg and larval components, then multiplying these weights against previously determined caloric values (Eldridge et al., 1980b). Yolk and tissue contents were measured directly. Oil globule contents were estimated by measuring globule volumes and comparing them against the initial globule volume in the egg prior to fertilization. Exogenous food intake was determined from counting stomach contents of larvae sampled 1 h after food introduction and entering these counts into the formula: FR = NH/D, where FR = ***daily food ration, N*** = average number of nauplii in stomachs, H = hours of active feeding, and D = digestion time. Other variables in the equation were previously determined and reported in Eldridge et al. (1980b). Routine metabolism was measured through oxygen consumption in a Gilson differential respirometer.

Sampling frequencies and sample sizes for different aspects of this study are summarized in Tables 1 and 2. Statistical summarizations, analyses and curve fittings were performed with the assistance of a CDC 7600 computer located at the University of California, Berkeley.

RESULTS

Exposure Concentrations

Actual aqueous benzene concentrations in test containers were higher than planned during embryonic prefeeding larva stages (Table 3) and the continuous exposure system proved more stable than the semi-static systems with its repeated daily dosages. Mean exposure concentrations ranged from 159 to 415 nll^{-1}. Prefeeding larvae were exposed to higher initial benzene concentrations than either embryos or feeding larvae (Table 3). Monitoring of benzene in the first 24 h after benzene introduction shows embryos in the continuous flow system had nearly

Table 3. Summary of benzene concentrations in culture containers of striped bass eggs and larvae

		Type of	Exposure concentrations		(nl l^{-1}, ppb)
Life Stage	Exposure Period	Exposure	$\bar{x}$	S.D.	Range
Egg	D-O to hatching (D-2)	Continuous	248	11	222-260
Prefeeding Larvae	D-2 to D-7	Semi-static	415	199	221-721
Feeding	D-8 to D-24	Semi-static			
	Fed Larvae	Semi-static	159	37	127-247
	Starved Larvae	Semi-static	159	19	127-187

constant benzene exposure (Table 4). Benzene is containers of later stages went through daily fluxes in which benzene was introduced with new water changes. Figure 1 illustrates how benzene decreased in a hyberbolic fashion in prefeeding larval containers and in exponential and linear declines in older stages.

Uptake, Accumulation and Depuration of Benzene in Tissues

In all life stages uptake and depuration of hydrocarbons were rapid, always within a matter of hours. All stages accumulated these hydrocarbons to levels greater than exposure concentrations and the longer the exposure, as in the older larvae, the greater the accumulation.

Table 4 presents results of embryonic uptake. Within an hour of benzene introduction embryos had accumulated over double the water concentration and this trend continued until newly hatched larvae had almost 18 times the average water benzene concentration. Depuration occurred quickly (Table 4). Embryonic tissues had only 57 plg^{-1} (ppb) within 12 h after the end of exposure.

The daily fluctuations of aqueous benzene in test containers of prefeeding larvae were reflected in tissue uptake (Table 4). Tissues reached equilibrium within 3 h after initial exposure then declined for the next 21 h, when the next dose of benzene was applied. Thus tissue benzene declined each day as aqueous benzene decreased. But larvae evidently were not able to completely eliminate benzene from tissues. Tissues sampled at the beginning of each day, before culture water was changed and new benzene added, had benzene in ever increasing amounts (Table 4).

Beginning with D-7 larvae were able to feed on live *Artemia salina* nauplii. This provided another pathway for benzene to enter larval tissues. Larvae deprived of food provided a way to estimate the contribution benzene-laden food made to tissue contamination. In the first 24-h larvae, as in earlier stages, rapidly accumulated benzene (Table 4). Equilibrium was reached within 3 h, the same as prefeeding larvae. But probably because of higher metabolic rates less benzene remained in tissues at the end of 24 h. For the remainder of the exposure period (D-9 to D-24) starved and fed larvae steadily accumulated amounts of benzene in their tissues (Fig. 2). This accumulation was best described by an exponential function in starved larvae and by a power function in fed larvae. After D-9 food appeared responsible

Table 4. Benzene concentrations in culture water and tissues of striped bass embryos, prefeeding and feeding larvae

Life Stage	Hours after initial exposure	Hours after end of exposure	Mean benzene concentrations	
			water ($nl\ l^{-1}$, ppb)	tissue ($pl\ g^{-1}$, ppb)
Embryo	0		250	—
	1		251	561
	3		257	1340
	6		250	1292
	12		239	2006
	24		256	411
	33		253	4512
	42		232	—
		1		991
		3		354
		6		237
		12		57
Prefeeding Larva	1		(see Figure 1)	2456
	3			2705
	6			2632
	12			1291
	24			1277
	72			2090
	120			3878
	144			4674
		1		991
		3		354
		6		237
		12		57
Feeding Larva Fed —	1		(see Figure 1)	1033
	3			2353
	6			603
	12			991
	24			175
Starved —	1		(see Figure 1)	1174
	3			868
	6			945
	12			338
	24			175

for higher accumulations of benzene.

In separate measurements of benzene uptake over a 24-h period by *Artemia* nauplii, we found nauplii also progressively took up benzene (Table 5). Their maximum accumulation occurred 6 h after initial exposure (4.5 x the initial

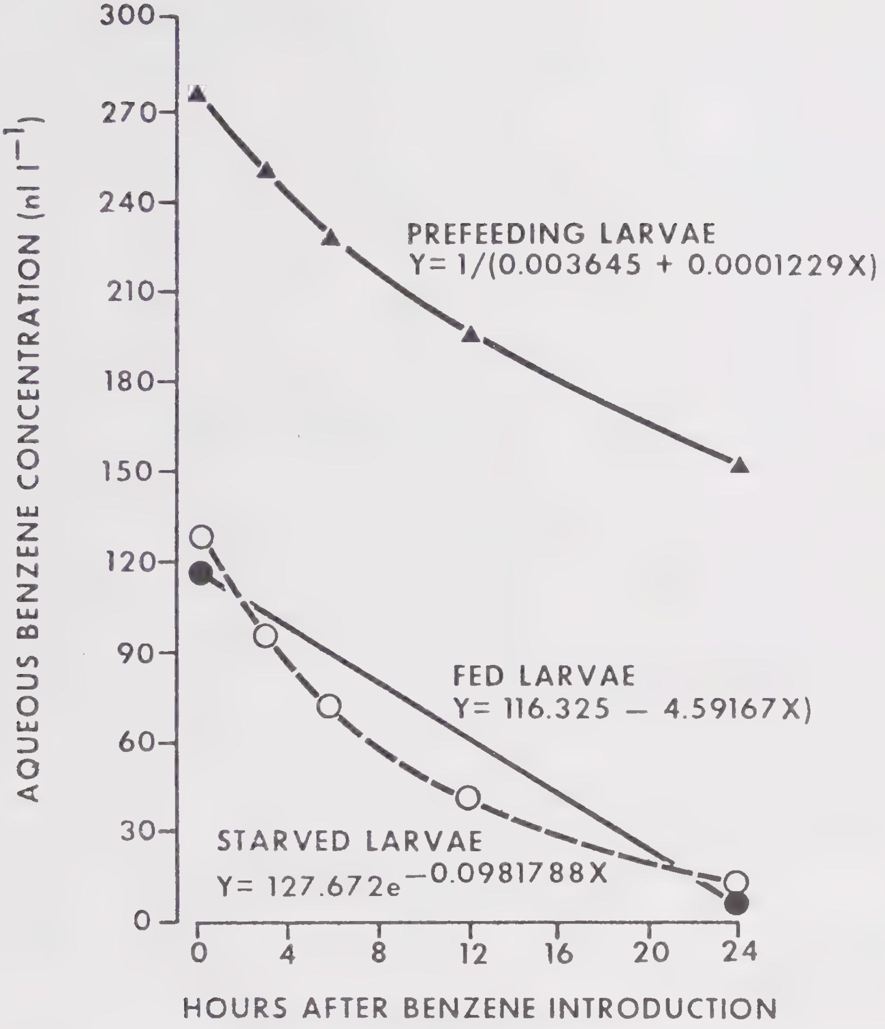

Figure 1. Benzene concentrations in test waters of prefeeding, feeding and starved larval containers during the first 24 h after initial exposure.

exposure concentration). Previous studies on striped bass larval feeding behavior indicate most of the daily food intake occurs within 10 h after food introduction (Eldridge et al., 1980b). Thus fish larvae fed on nauplii when they were most contaminated.

Concentration Factors

Differences in the maximum amounts of benzene accumulated in tissues of various life stages are presented in Table 6. Older, feeding larvae took up much more benzene, and thus achieved higher concentration factors than either prefeeding larvae or embryos. While embryos and prefeeding larvae had approximately the

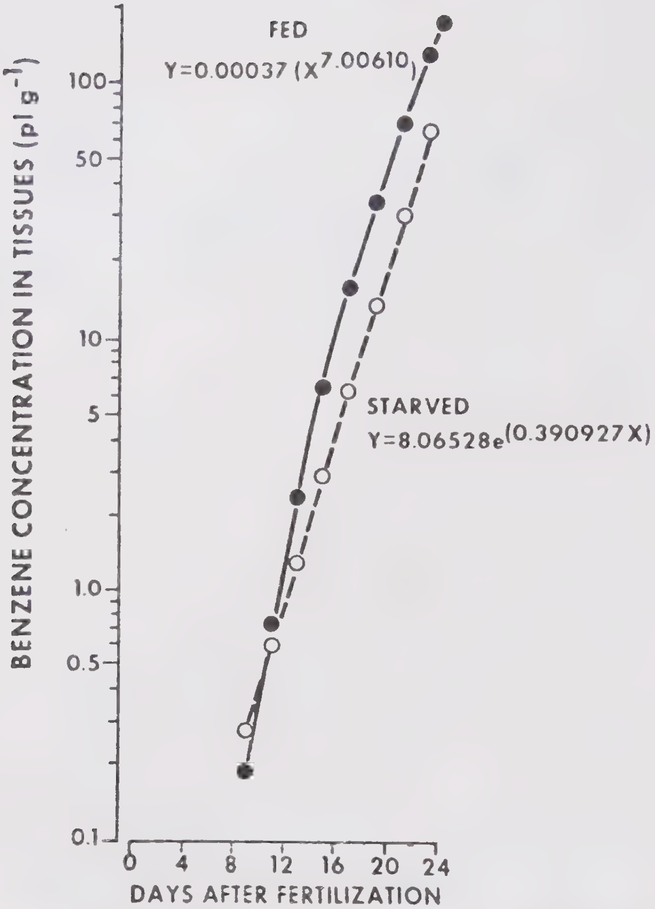

Figure 2. Benzene concentrations in the tissues of feeding and starved larvae from 7 to 29 days after fertilization.

same maximum tissue concentrations, feeding larvae never stopped accumulating benzene.

Survival

Embryos exposed to benzene had lower mortalities to hatching than unexposed (Table 7). Forty-six percent of exposed embryos successfully hatched as compared to 38% of controls. Benzene also caused earlier hatching; total hatching of exposed embryos was completed 5 h before that of controls. Despite better survival to hatching, larvae previously exposed in the embryo stage showed mortality rates higher than unexposed (Table 7) and fewer larvae made successful transition to active feeding.

All prefeeding larvae suffered from high mortality from D-4 to D-6. For the entire 5-day stage, exposed larvae died at rates twice as high as unexposed (Table 7). Delayed mortalities in both treatments were low. The few remaining exposed larvae

Table 5. Concentrations of C^{14}-benzene in culture water and tissues of *Artemia salina* nauplii over a 24-h period

Hours after Initial Exposure	Water (nl l^{-1})	Tissue (nlg^{-1})
0	206	0*
1	194	320
3	172	312
6	150	918
12	109	557
24	59	702

*Below levels of detectability with our analytical method.

Table 6. Maximum accumulations and concentration factors of benzene in tissues of different life stages of striped bass

Life Stage	Means aqueous concentrations	Maximum tissue concentrations (plg^{-1})	Concentration factor
Embryo	138	4512	32.7
Prefeeding Larvae	415	4674	11.3
Feeding Larvae	159	226155	1422.4
Starved Larvae	159	73663	463.3

did have more larvae survive to D-29 than controls.

Essentially no effects from benzene exposure were seen in the survival of fed larvae, either during or after exposure (Table 7). Starved larvae, however, died in higher numbers in exposed treatments and near total mortality occurred by the end of the exposure period (D-24).

Growth

We found no significant differences in the sizes of newly hatched larvae from exposed and unexposed eggs. Standard length of exposed averaged 3.6 mm versus 3.5 mm for controls. Assimilated tissues amounted to 34 μg in exposed and 33 μg in controls. Growth of larvae from exposed eggs did achieve larger sizes than unexposed during the period D-2 to D-27. Daily instantaneous growth coefficients ($G_w = \ln (SL_i - SL_3) / T$, where SL_i = initial size at beginning of test period, SL_e = size at end of test period, T = number of days in test period) for exposed were 0.072 and for control, 0.060.

Table 7. Daily instantaneous mortality* coefficients of striped bass embryos prefeeding larvae and feeding larvae under different benzene exposure conditions

Life Stage	Experimental Condition	Age (days)†	Benzene exposed	Unexposed
Egg	during exposure	0-2	.384	.485
	after exposure	3-29	.111	.085
Prefeeding Larvae	during exposure	2-7	.599	.241
	after exposure	8-29	.028	.050
Feeding Larvae	during exposure	8-23	.024	.029
	after exposure	24-29	-0-	-0-
Starved Larvae	during exposure	8-23	.200	.126
	after exposure	24-29	N/A‡	.081

*Daily instantaneous mortality = $\ln (N_i T - N_e)$. where N_i = initial number of embryos or larvae. N_e = number of animals at end of test period, and T = days in test period.

†Days after fertilization

‡Only 1 animal left for this experimental period.

Larvae growth in the short 5-day exposure period of the prefeeding larva stage was similar to that of the embryonic period — no significant differences due to benzene exposure. G_w values by standard lengths were the same (0.118) for both treatments. Larval dry weights were also indistinguishable (77 μg for exposed and 80 μg for controls). Later growth to D-27 was faster in exposed ($G_w = 0.073$) than controls ($G_w = 0.060$).

The effects of benzene on growth of larvae after D-8 was readily apparent (Fig. 3), not so much in their standard lengths as in tissue dry weights. After what appeared as a brief adjustment period from D-7 to about D-15, exposed larvae became longer and heavier. By D-29 controls had achieved the same lengths as exposed larvae but they remained lighter in weight.

Bioenergetics

Endogenous energy sources of striped bass eggs are comprised of yolk and oil (Eldridge et al., 1980a). Through standard calorimetric methods we determined the average caloric content of the eggs at the time of fertilization to be 2.231 calories per egg. Original yolk energy content was 0.537 calories and oil energy content 1.694 calories.

In the 2-day embryonic test period, benzene caused almost identical energy consumption of yolk and oil calories. Exposed embryos used 36% of its yolk energy and 26% of its oil energy. Control embryos used slightly less yolk, 31%, and 27% of its oil. After hatching larvae from exposed eggs did not differ from controls in their utilization of yolk and oil energies. All yolks were consumed by D-7. Oil globule

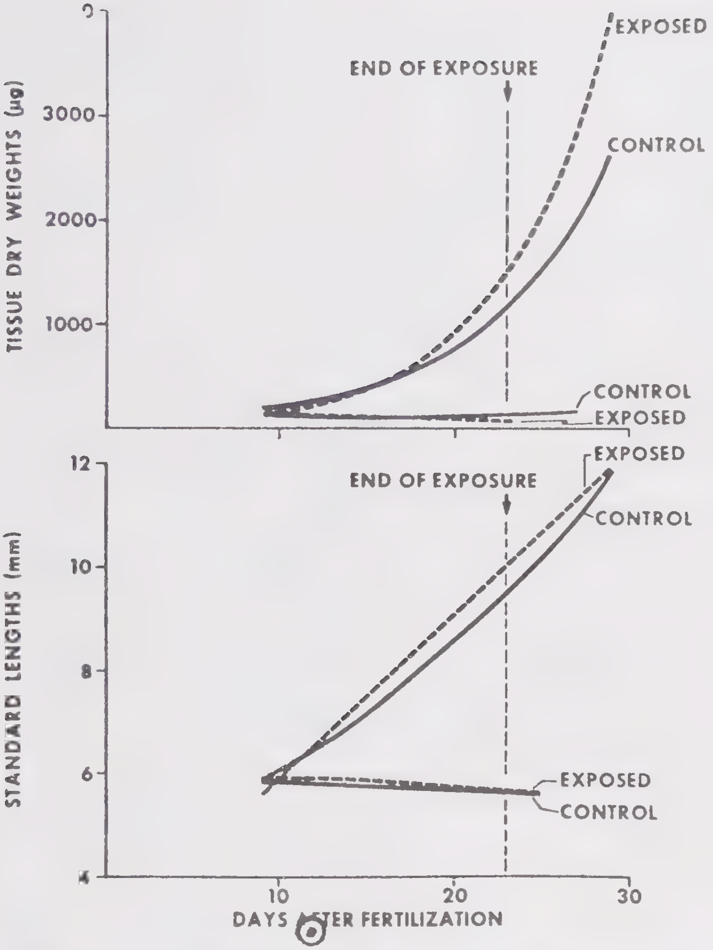

Figure 3. Tissue dry weights and standard lengths of striped bass larvae from 7 to 29 days after fertilization.

energy was used slowly and for a longer period in larvae from exposed eggs. Traces of oil were measured in these larvae to D-21 and only to D-17 in control larvae.

Endogenous energy consumption in prefeeding larvae also had no major differences due to benzene. Yolk from hatching to consumption was used at hyperbolic rates by both treatments. During exposure oil consumption was slightly faster in controls but larvae reared to metamorphosis actually retained their oil globules longer (to D-23 as opposed to D-21). Best fit equations for oil consumption were $Y = 1.304-0.056\ X$ for controls and $Y = 1.516-.068\ X$ for exposed, where Y = oil calories and X = age in days after fertilization.

Endogenous energy for older, feeding larvae came solely from the oil globule. No significant differences were seen in the consumption of this energy in either starved or fed animals (Fig. 4). Though not statistically different, starved larvae exposed to

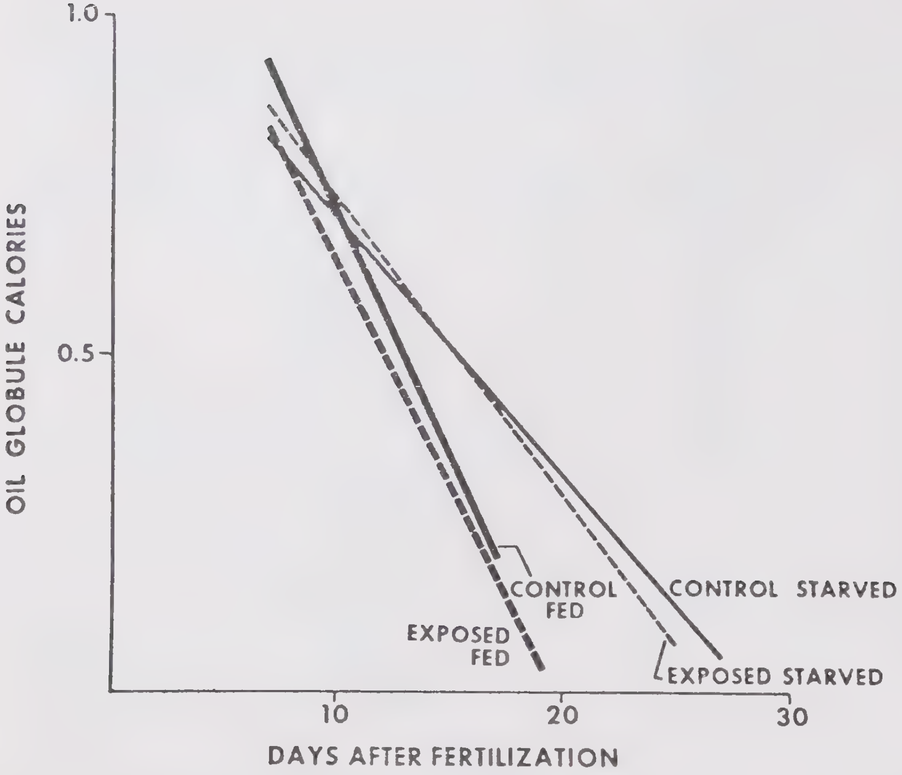

Figure 4. Oil globule calories in striped bass larvae 7 to 29 days after fertilization.

benzene had a faster use rate than controls ('b' value for exposed was -0.044 for exposed and -0.039 for controls). Fed larvae have previously been found to use their oil energies at faster rates than starved animals (Eldridge et al., 1980b). Controls were found to have slightly faster use rates (b = -0.074) and exhausted their oil 2 days before exposed animals (b = -0.067).

Exogenous energy input was estimated for feeding larvae by counting larval stomach contents and using a formula for daily food ration (D.F.R. = (stomach contenst) x (hours of active feeding)/digestive time). Values for feeding time and digestion were predetermined (Eldridge et al., 1980b). Exposure to benzene seemed to reduce the numbers of larvae successfully feeding up to about D-17 (Table 8). After D-17, unexposed were less or about the same. The daily food rations of controls exceeded those of exposed; 7 of 10 ration estimates showed controls with larger rations.

Oxygen consumption was markedly elevated by benzene (Fig. 5). On a weight specific basis benzene increased metabolism in all life stages. Figure 5 also shows the

Table 8. Feeding incidence (percent of sampled specimens with identifiable food in stomach) and estimated daily ration (given in numbers of *Artemia salina* nauplii and equivalent calories)

Age (Days after fertilization)	Percent with food in stomach		Daily food ration			
	Control	Exposed	Control		Exposed	
			Number of Nauplii	Calories	Number of Nauplii	Calories
9	90	40	49.5	0.476	15.2	0.146
11	70	70	34.2	0.329	29.0	0.279
13	100	100	68.8	0.661	63.3	0.609
15	70	50	59.4	0.571	32.7	0.315
17	90	70	57.9	0.556	57.9	0.556
19	30	70	12.1	0.116	14.2	0.137
21	50	60	20.6	0.198	19.1	0.183
23	100	100	178.5	1.715	112.1	1.077
25	100	100	240.6	2.312	267.9	2.574
27	100	50	170.9	1.642	32.1	0.309

larger sizes attained by exposed larvae.

DISCUSSION

Developments in analytical capabilities have allowed scientists to detect extremely low concentrations of aromatic hydrocarbons, including benzene, in waters where previously they were believed to have volatilized. Results of our study demonstrated that planktonic striped bass eggs and larvae take up benzene at low sublethal concentrations and accumulate it to levels many times that of the surrounding water. Early life stages of other fish species have also been found to accumulate benzene and related monoaromatic hydrocarbons. They did not, however, concentrate them to such high degrees and they differed in the life stages which took up the most hydrocarbons and the times required to reach equilibrium. In a study by Eldridge et al. (1977) Pacific herring eggs and larvae all reached equilibrium with benzene within 6-12 h. Eggs accumulated the most benzene, 10.9 times the initial concentration, yolksac larvae, 6.9 times, and feeding larvae, 3.9 times. The reverse pattern was found by Korn and Rice (1980). Coho salmon alevins preceded fry, which exceeded eggs in the uptake and accumulation of toluene. No stage achieved a concentration factor higher than about 20. Salmon eggs required 10 days to reach equilibrium, alevins around 36 h, and fry only 3 h. Striped bass eggs, in continuous exposure, never reached an equilibrium state by hatching. Later larval stages did likewise. We believe striped bass continued to accumulate benzene

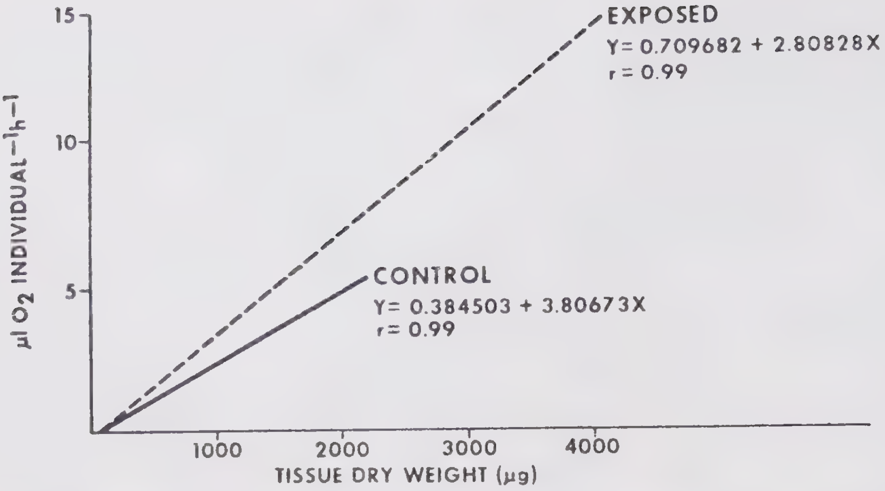

Figure 5. Oxygen consumption of striped bass embryos and larvae from fertilization to 29 days after fertilization.

because of its extraordinary high amount of oil, located mainly in the oil globule. Fifty two percent of the embryo's total dry weight consists of this oil (Eldridge et al., 1980a). Older larval stages may relocate these lipid stores in other areas of their bodies as oil globules are consumed.

Greater amounts of benzene in tissues of feeding larvae as compared to starved larvae and the uptake of benzene measured in *Artemia* nauplii lead us to conclude that ingested contaminated food served as a pathway for benzene into larval tissues. Herring larvae feeding on live rotifers showed similar results (Eldridge et al., 1977; Echeverria, 1980). Nonetheless benzene in water still appears to be the principal source of the hydrocarbon.

Among the effects due to exposures to low level sublethal concentrations of benzene (Table 9) direct mortality was not readily apparent. Delayed mortalities occurred in larvae from exposed eggs, exposed prefeeding larvae had slightly higher mortalities, and feeding larvae did not seem affected. The older starved larvae, however, suffered most from the added stress of benzene. Their behavior was different from unexposed, starved larvae in that they were much less active and they died much sooner than their unexposed counterparts. This suggests that larvae feeding on less than maximum food rations have a potential for higher mortalities.

Growth of feeding larvae, measured in tissue weight, was definitely advanced by benzene exposure. Similar findings were found by Eldridge et al., (1977) in Pacific herring exposed to low benzene concentrations. The proposed explanation for the herring results seems also appropriate with striped bass. That is, benzene in low chronic doses stimulates adaptive physiological responses which are often measured in what might be interpreted as beneficial mode. The hypothesis is termed "sufficient challenge" (Smyth, 1967).

Among the energetic variables measured, the consistently higher metabolism of exposed animals is most noteworthy. Brocksen and Bailey (1973) found that low concentrations of benzene increased oxygen consumption in striped bass juveniles.

Table 9. Summary of multi-disciplinary study on the effects of low level concentrations of benzene on early lifestyles of striped bass

Life Stage	Uptake accumulation and depuration	Mortality	Growth	Bioenergetics		
				Endogenous Energy	Exogenous Energy	Metabolism
Embryo	Rapid and continuous uptake; 33x concentration factor; rapid release.	Benzene enhanced survival to hatching but offset by delayed mortality.	No effects during exposure; larvae from exposed egg larger.	No distinct differences.	—	Benzene caused increase.
Prefeeding larvae	Rapid uptake; gradual accumulation; lowest concentration (11x) factor.	Benzene increased mortality during exposure.	No effects during or after exposure	Slightly faster oil utilization in controls.	—	Benzene caused increase.
Feeding larvae	Rapid uptake and rapid loss; continuous accumulation; benzene entered tissues via food; very high concentration factor in fed larvae (1422x).	No effects on fed larvae; starved larvae suffered high mortalities from benzene.	More tissue assimilation due to benzene.	Benzene slightly enhanced oil consumption in fed larvae.	Benzene reduced feeding incidence and ration amounts.	Benzene caused increase.

Evidently low level chronic concentrations of benzene elicit resistent stress responses. In the general adaptation syndrome (G.A.S.) caused by stress, animals first have an alarm reaction followed by a stage of resistance. If the stress is highly concentrated or prolonged, a stage of exhaustion then takes over (Selye, 1950). We hypothesize that the high metabolic rates and possibly the increased growth caused by low benzene concentrations are due to the animals being in the second stage of the G.A.S., that of resistance. Exposed striped bass embryos and larvae accelerate development (i.e., early hatching, faster anabolism) since it is to the animal's advantage to grow and differentiate so as to increase its resistance capabilities (such as increased mobility, detoxification capability). The sufficient challenge effect is then interpreted as a resistance reaction which, over the short term, more than meets the needs to counter the stress and temporarily benefits the animal. Prolonged exposure could eliminate these benefits if the animal becomes exhausted. To fully explore this possibility it will be necessary to expose early life stages through and beyond metamorphosis.

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Effects of Food and Feeding Factors on Laboratory-Reared Striped Bass Larvae

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Abstract

Fluctuations in year-class size of striped bass (*Morone saxatilis*) are believed related to early-life-stage mortality. Factors associated with food and feeding of larvae were studied in the laboratory as they relate to mortality, point of no return, development, and energetics. Mortality of feeding larvae was directly related to density of *Artemia salina* nauplii. Highest mortality coincided with total oil globule absorption. Starved larvae lived an average 31 days after fertilization and did not display a well-defined point of no return. Growth and differentiation directly correlated with food density. Starvation affected the rate of ossification and altered cells and tissues as early as 7 days after hatching. Most of the endogenous energy of newly fertilized eggs is in oil. The rate of oil utilization was inversely related to food density. Daily food rations were estimated after ingestion and digestion rates were determined, and increased with larva size, age, and prey density.

Between 1879 and 1882, 432 juvenile striped bass (*Morone saxatilis*) from the Navesink River, New Jersey, were released into the San Francisco Bay-Delta estuary. The transplant was so successful that, within 10 years, the commercial fishery landed 554 t (Skinner 1962). In less than 100 years, the Pacific range of striped bass has expanded south to 30 km below the United States-Mexico border and north to Barkley Sound, British Columbia (Miller and Lea 1972).

Over the intervening years, sport and commercial catch records have indicated considerable fluctuations in the Pacific striped bass population (Smith and Kato 1979), and present estimates place the population at 33 to 40% of its peak 1960 estimate of 3.0 to 4.5 × 10^6 fish. Recent field data indicate that mortality during the first 60 days after hatching determines the size of the adult population. Further, abundance of young-of-the-year juveniles is directly related to river outflows and diversion volumes in the Sacramento-San Joaquin River Delta (Chadwick et al. 1977). However, aside from direct export of eggs and larvae out of the estuary via water diversions, the actual causes of mortality remain undetermined. As part of a cooperative research program involving the California Department of Fish and Game, the United States Water and Power Resources Service, and the National Marine Fisheries Service, we have conducted laboratory studies of mortality factors associated with larval food and feeding. Among marine fish larvae, starvation and food and feeding factors are primary causes of mortality (Hunter 1976). This paper summarizes our analyses of food-related mortality and development, and other related features of striped bass larvae.

Methods

Adult striped bass in spawning condition were electrofished in the Sacramento River, injected with human chorionic gonadotropin by methods of Bayless (1972), and transported to the California Department of Fish and Game Central Valleys Hatchery, Elk Grove, California. Mature gametes were stripped from these adults within 26–36 hours. To ensure known percentage of each of nine pairings, eggs from a single female were fertilized with sperm from a single male. Newly fertilized eggs were allowed to water-harden 1.5–2.5 hours. We then transported them to the Tiburon Laboratory where they were incubated in McDonald jars in dechlorinated tap water at 18 C.

Hatching occurred within 48 hours as Rogers et al. (1977) found. Newly hatched larvae were placed in semispherical green acrylic plastic containers filled with 8 liters of water; the containers were placed in water tables. Larva densities differed among studies. In survival studies, two replicate containers with 25 larvae in each were used. Larvae used for growth and development were stocked at 100 larvae per container at four replicates per food concentration. To approximate natural water quality conditions, salinity was maintained at 1‰ from 6 to 13 days after fertilization and at 3‰ from day 14 until the completion of each experiment. Under average conditions in the San Francisco Bay-Delta estuary, striped bass eggs and prefeeding larvae migrate from upstream waters less than 0.5‰ salinity to approximately those of 1.0‰ within 6 to 7 days after spawning. Larvae then move into shallow nursery areas where average salinities increase 1–3‰ depending on tidal flow and river discharge (Conomos et al. 1979). Water temperatures were maintained at 18.0 ± 0.5 C (±range) and dissolved oxygen was stable at or near saturation.

Larvae were given newly hatched *Artemia salina* nauplii at initial concentrations of 0.00, 0.01, 0.50, 1.0, and 5.0 nauplii/ml; there were two replicate containers per food concentration. These food densities range above and below the estimated field concentration of 0.10 zooplankter/ml (Daniel 1976). Food and water were changed daily in each container.

The "point of no return," the time when starved larvae will not feed even when food is introduced (May 1974), was determined by holding larvae without food (25 larvae per container, two replicates) for 10, 14, 18, 22, 26, and 28 days before nauplii were presented to them. Daily survival and size at the age of 31 days after fertilization were measured.

Development was monitored by removing eggs at 12-hour intervals during incubation, by sampling larvae daily from hatching to day 7 (time measured from fertilization), and by sampling feeding larvae on alternate days until the end of the experiments. Morphometric measurements were made with an ocular micrometer. Dry weights of assimilated tissues, yolk, and chorions were obtained by careful dissection of eggs and larvae, drying for 24 hours at 60 C, and measurement on a microbalance. Oil weights were estimated by subtraction of the weighed body components from total weights. A developmental series was differentially stained for cartilage and bone development with Alcian blue and Alizarin to monitor ossification. Another developmental series was fixed in Bouin's solution, stained with hematoxylin and eosin, and sectioned in 7-μm longitudinal and cross sections.

Bioenergetic studies followed procedures of Eldridge_1 et al. (1977). Feeding rates were determined by introducing food to larvae held without food for 24 hours, and by removing and examining larvae at 2-hour intervals. Digestion rates were determined by feeding dyed nauplii to larvae for 1.5 hours, replacing uneaten dyed nauplii with unmarked ones (so that larvae could continue feeding), and examining anesthetized larvae every half hour. The dyeing procedure consisted of allowing nauplii to feed on dense cultures of *Nephroselmis* sp. until the intestinal tract was pigmented dark green. In this way, we measured the time required for dyed foods to pass through the digestive tracts of actively feeding larvae.

Results

Mortality

Estimation of mortality during the embryonic and prefeeding larval stages was difficult because spawning success varied greatly. In three spawning seasons, only five of nine spawnings were sufficiently successful to allow us to rear striped bass to metamorphosis. In the four unsuccessful spawnings, nearly 100% mortality occurred, most taking place 12–18 hours after fertilization. In contrast, embryos and larvae in the successful spawnings had high (>80%) survival up to the time of feeding.

For this reason, quantitative emphasis was given to mortality during the larval feeding stage, from 7 to 31 days after fertilization. Survival was directly related to food concentration (Fig. 1). The average daily instantaneous mortality (Y) was inversely correlated ($r = 0.85$) with food concentration (X), and was best described by the equation $Y = 1/(41.90 + 27.56X)$:

Nauplii per milliliter	Instantaneous daily mortality
0.00	0.12
0.01	0.051
0.10	0.027
0.50	0.013
1.00	0.008
5.00	0.006

The overall survival pattern of larvae at all food densities was similar. The small decrease in sur-

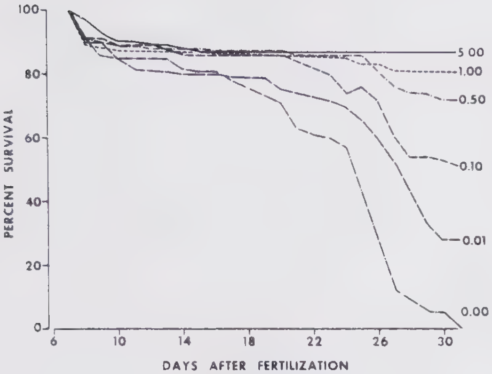

FIGURE 1.—*Survival of striped bass larvae feeding on six different food concentrations of* Artemia salina *(0.00–5.00 nauplii per milliliter).*

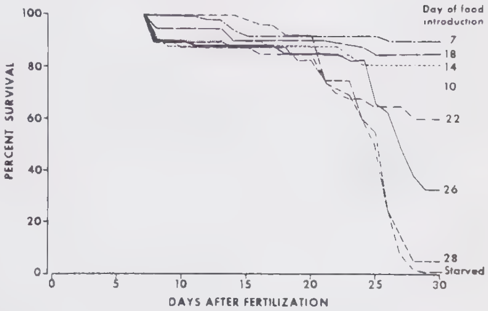

FIGURE 2.—*Survival of striped bass larvae given initial food at progressively later ages (7–28 days after fertilization).*

vival after food introduction is presumably an adjustment to feeding. Increased mortality rates occurred at all food concentrations after day 18, except among larvae at the highest food density (5.0 nauplii/ml), coinciding with the total absorption of the oil globule. Starved larvae demonstrated remarkable resistance to food deprivation by living for 31 days after fertilization.

Point of No Return

Larvae did not display a well-defined point in time when they were not able to successfully ingest and utilize food. Over 70% of the larvae given food on and before 18 days after fertilization survived (Fig. 2). Larvae deprived of food for longer periods appeared to undergo an adjustment when weaker larvae died. Mortality then stabilized, but at progressively lower levels. We observed that survival seemed to depend on the larva's ability to capture prey, which was a function of prey density and remaining strength. Size of larvae on day 31 was inversely related to their age at first food introduction (Table 1). As in mortality, larvae deprived of food from age 18 days or less grew to approximately similar lengths. Comparative weights reflected starvation times more clearly than lengths.

Development

Growth, as measured by tissue dry weight, was linear for embryos and larvae up to the time of feeding (Fig. 3). Newly hatched larvae averaged 3.4 mm standard length (SL) and length increased hyperbolically to 6.0 mm by day 7 when they began feeding (Fig. 4).

Growth rates of larvae correlated with food concentrations (Fig. 4). Below 0.10 nauplii/ml (the estimated concentration of zooplankton in the delta), larvae decreased in size and growth rates were negative. Food concentrations higher than 0.10 nauplii/ml resulted in increased growth rates, the highest being at food concentrations of 5.0 nauplii/ml.

Rates, rather than sequences, of larval differentiation were markedly affected by food density. Our differential staining technique distinguished cartilage from endochondral bone that preforms in cartilage. When larvae began to feed 7 days after fertilization, they exhibited extensive cartilage in the branchiocranium.

TABLE 1.—*Mean sizes ± SD of striped bass larvae on day 31 following delayed first feeding.*

	Age at food introduction (days from fertilization)					
	7	10	14	18	22	26
Standard length (mm)	10.8 ± 0.5	11.4 ± 0.5	10.4 ± 0.8	9.0 ± 1.2	7.4 ± 0.8	6.1 ± 0.3
Dry weight (μg)	7.12 ± 0.10	5.83 ± 0.18	3.43 ± 0.40	1.54 ± 0.70	0.36 ± 0.17	0.14 ± 0.02

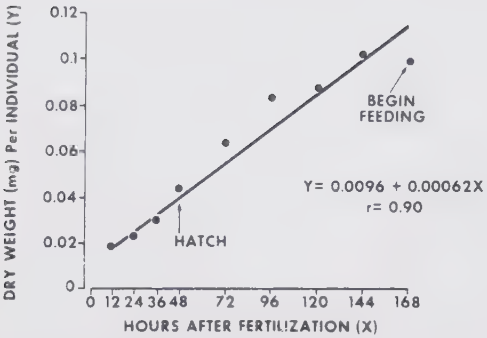

FIGURE 3.—*Dry weight of dissected tissue of striped bass embryos and prefeeding larvae.*

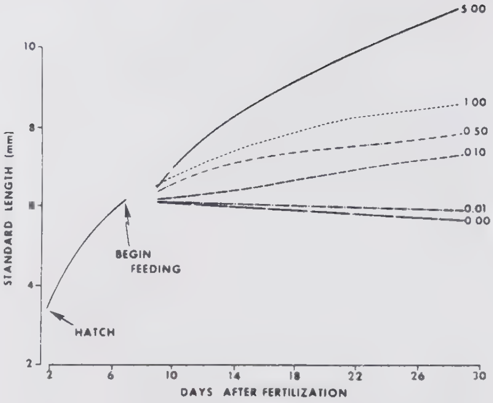

FIGURE 4.—*Standard lengths of striped bass larvae feeding on six concentrations of* Artemia salina *(0.00–5.00 nauplii per milliliter).*

The upper and lower jaw bones, cleithrum, branchiostegals, and bases of the pectoral fins (coracoid and scapula) were well formed in cartilage. In the absence of food and at the lowest food concentration (0.01 nauplii/ml), no change in the amount of cartilage or ossification was seen for 31 days, when the remaining larvae died. In larvae fed 5.0 nauplii/ml, ossified bones were found as early as day 9. The rate of ossification was slower with each decrease in food concentration. In all cases, ossification began in the cleithrum, premaxillary, maxillary, and dentary bones.

Examination of sectioned larvae revealed differences in cells and tissues between fed and starved larvae beginning as early as day 9. Most obvious were the deterioration and disintegration of cells in tissues associated with the digestive tracts of starved larvae (Fig. 5). Tissue conditions of starved larvae closely paralleled those reported for jack mackerel, *Trachurus symmetricus*, and northern anchovy, *Engraulis mordax* (O'Connell 1976; Theilacker 1978).

Energetics

The endogenous energy sources of striped bass embryos and larvae consist of yolk and oil, the latter in the form of a single large globule (Fig. 6). These egg constituents, as well as total weights, varied considerably among females (Table 2). Eggs initially weighed 285 μg with a coefficient of variation of 19% (100·SD/mean). The average energy available to the beginning embryo was 2.068 calories. Although the oil contributed 55% of the egg weight, it supplied 72% of the total egg energy at 9,441 cal/g. Proteinaceous yolk (5,404 cal/g) was 38% of egg weight, but accounted for only 28% of total energy.

Larvae used their yolk reserves first (Eldridge$_2$ et al. 1977). Total yolk absorption coincided with the onset of feeding on day 7. The efficiency of energy conversion to this point of development was 56.2%. To hatching it was 53.9%. The rate of utilization of the remaining oil was inversely related to the amount of food available; starved larvae retained their oil globule for the longest period while fed larvae channeled oil energy into feeding and development (Fig. 7).

Estimates of exogenous energy utilization, expressed as daily food ration, required information on food intake and digestion rates. In our experimental conditions, larvae fed most actively the first 10 hours after food introduction (Fig. 7). Limited feeding occurred at night. Day-12 larvae were the most active nocturnal feeders. Prey densities related most directly to feeding rates in the oldest larvae. Larvae in low food densities consistently fed at the lowest rates, while larvae in higher densities varied more. Larvae with the most food available (5.0 nauplii/ml) fed at lower rates at ages 12 and 21 days, but were seen to extend their feeding well into the night.

The time required for a unit of food to pass through the digestive tract of a larva under experimental conditions of continuous feeding ranged from 1.5 to 5.5 hours (Table 3). Times varied considerably and patterns were not

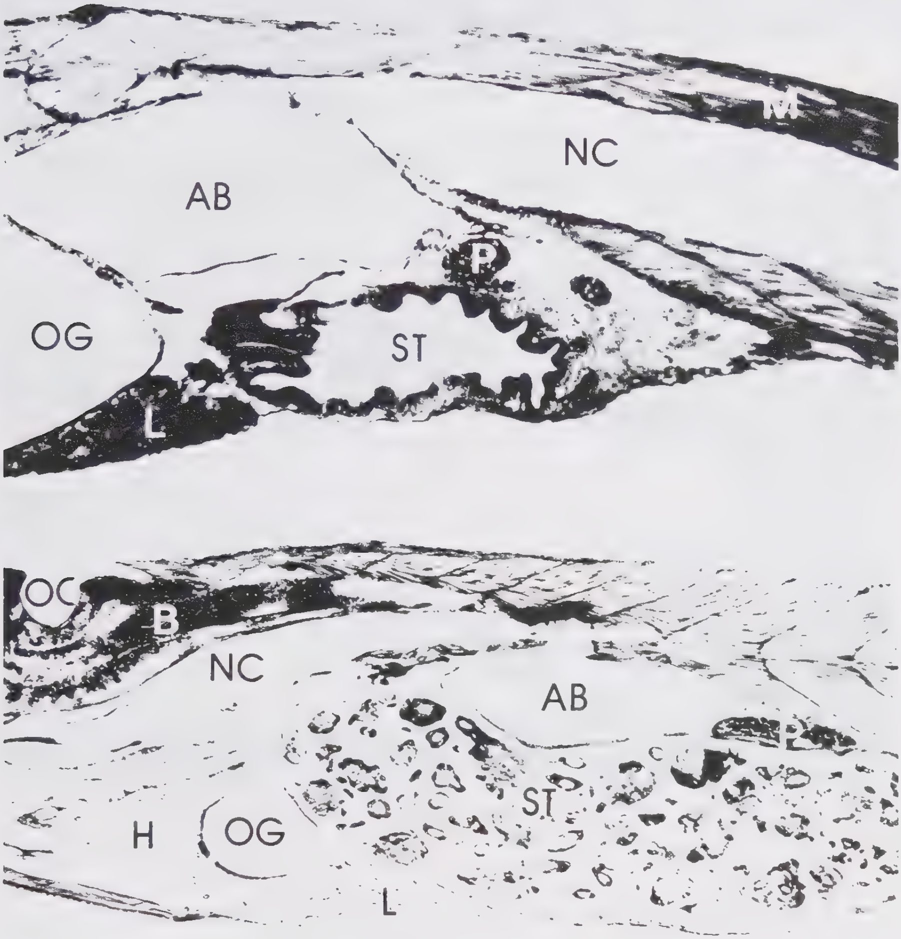

FIGURE 5.—*Longitudinal sections through midsections of 21-day-old starved (above) and fed (below) striped bass larvae. AB = air bladder; B = brain; H = heart; L = liver; M = muscle; NC = notochord; OC = otic capsule; OG = oil globule; P = pancreas; ST = stomach.*

readily apparent. When data are combined, digestion generally appeared to be shorter at the middle ages in all food concentrations. Larger larvae feeding in the two higher food densities had progressively lower digestion times.

From the above feeding and digestion rates we calculated daily food rations according to the formula: $FR = NH/D$, where FR = daily food ration, N = average number of nauplii in stomachs, H = hours of active feeding, and D = digestion time. The results were also expressed in calories and equivalent numbers of zooplankters (Table 4). The latter figures were calculated from relative compositions of different food items (unpublished data, California Department of Fish and Game) in guts of wild larvae and their caloric values (Cummins 1967; Laurence 1974). Daily rations increased with larva size and age, and prey density. In the two high food densities, the ration actually decreased between the 21- and 33-day larvae. This was most likely a result of limited food supply for the older larvae because they were

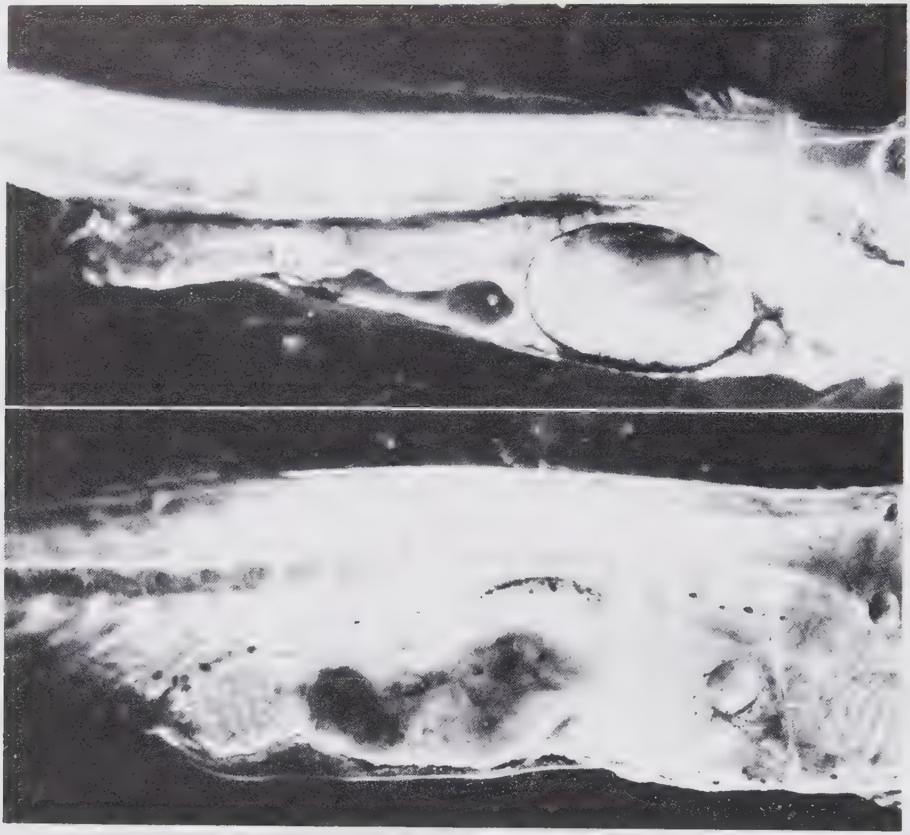

FIGURE 6.—*Photomicrographs of live striped bass larvae 19 days after fertilization. Note different sizes of oil globules in starved (above) and fed (below) larvae.*

more efficient feeders and grazed the finite food supply more quickly.

Discussion

Major findings of our research are in general agreement with comparable studies (Daniel 1976; Lal et al. 1977; Miller 1977; Rogers and Westin 1977; Rogers et al. 1977; Rogers 1978).

Greatest mortality of striped bass larvae occurs when the endogenous energy source (yolk and oil) is exhausted. Differences in the ages of larvae when mortality rates were highest are

TABLE 2.—*Dry weights and caloric contents of six unfertilized striped bass eggs.*

	Dry weight (μg)				Caloric content (cal)		
Egg	Yolk	Oil	Chorion	Total	Yolk	Oil	Total
1	0.089	0.128	0.014	0.231	0.481	1.208	1.689
2	0.131	0.089	0.028	0.248	0.708	0.840	1.548
3	0.089	0.137	0.023	0.249	0.481	1.293	1.774
4	0.114	0.150	0.022	0.286	0.616	1.416	2.032
5	0.118	0.189	0.014	0.321	0.638	1.784	2.422
6	0.106	0.251	0.016	0.373	0.573	2.370	2.943
Mean ± SD	0.108 ± 0.017	0.157 ± 0.056	0.019 ± 0.006	0.285 ± 0.054	0.583 ± 0.090	1.485 ± 0.530	2.068 ± 0.528

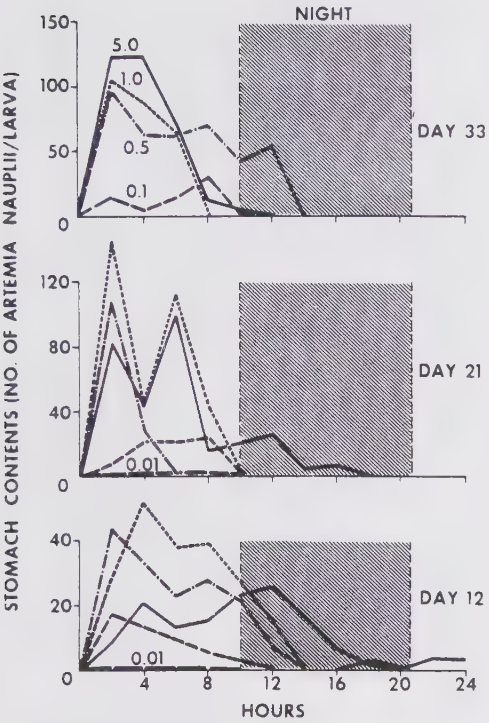

FIGURE 7.—*Twenty-four-hour feeding rates of striped bass larvae of three ages fed five concentrations of* Artemia salina *(0.01–5.00 nauplii per milliliter). Larvae fed 0.01 nauplii per milliliter had died by day 33.*

TABLE 3.—*Digestion rates (hours/larva) of striped bass larvae fed different concentrations of dyed* Artemia salina *nauplii. Hours to 50 and 100% signify time required for either half or all of sampled larvae to completely evacuate dyed nauplii.*

Prey concentrations (nauplii/ml)	Larva age (days from fertilization)	Larva standard length (mm)	Evacuation	
			Hours to 50%	Hours to 100%
		Experiment 1		
0.01	11	5.7	3.0	3.0
	20	5.6	1.5	2.5
0.10	11	6.0	3.5	4.5
	20	6.3	2.0	3.0
	33	9.3	2.0	2.0
0.50	11	6.7	3.5	4.0
	20	7.3	3.5	5.0
	33	8.0	4.5	4.5
1.00	11	6.7	2.5	3.5
	20	7.5	3.5	4.5
	33	8.2	5.0	5.0
5.00	11	7.0	2.0	2.5
	20	9.6	2.0	2.5
	33	10.8	2.5	3.0
		Experiment 2		
0.01	9	6.1	3.5	3.5
	20	5.9	1.5	1.5
	28	6.1	2.5	2.5
0.10	9	6.3	3.0	3.5
	20	6.7	2.0	2.5
	28	6.7	3.0	3.0
0.50	9	6.3	3.0	3.0
	20	7.6	1.5	2.0
	28	7.6	2.5	3.0
1.00	9	6.4	4.0	5.5
	20	8.1	1.0	2.5
	28	9.4	3.0	3.0
5.00	9	6.4	4.0	5.5
	20	9.9	1.0	2.0
	28	10.6	2.5	3.0

attributable to differences in times of total yolk and oil absorption.

Larva survival is related to food availability. This relationship was supported by other studies (Daniel 1976; Miller 1977) despite different prey concentrations and experimental conditions.

Striped bass larvae are highly resistant to food deprivation as evidenced by their long survival times when starved and the apparent absence of a "point of no return." Rogers and Westin (1981) had similar results in studies of east coast striped bass. The absence of a point of no return has only been noted in bairdiella, *Bairdiella icistia* (May 1971) and California grunion, *Leuresthes tenuis* (Ehrlich and Muszanski, in press). Miller (1977) concluded the point of no return for striped bass was 10 days after hatching. We believe the rearing conditions in his system were more stressful than in either Rogers (1978) or ours, such that overall survival was probably affected. The biggest contrast was in the smaller rearing containers, higher stocking densities for larvae and food, and the use of fresh water throughout his experiment. In particular, we found a gradual increase of salinity, as is normal for striped bass, to be beneficial.

Development of striped bass larvae, as measured by growth and differentiation, is directly correlated with prey concentration. The growth rates of our larvae fed at the highest concentration compared favorably with those of wild and laboratory-reared striped bass for the same developmental period (Mansueti 1958; Hum-

TABLE 4.—*Daily food rations (expressed in numbers of* Artemia salina *nauplii, equivalent calories, or equivalent wild zooplankters consumed per larva per day) of striped bass larvae fed different concentrations.*

Prey concentration (nauplii/ml)	Larva age (days from fertilization)	Daily food ration		
		Nauplii	Calories	Wild zooplankton
0.01	12	0.3	0.003	0.4
	21	1.9	0.018	2.5
0.10	12	22.8	0.218	29.9
	21	28.7	0.274	37.6
	33	66.0	0.630	86.5
0.50	12	79.5	0.759	104.3
	21	56.4	0.539	74.0
	33	173.3	1.655	227.4
1.00	12	115.6	1.104	151.7
	21	151.0	1.442	198.1
	33	102.7	0.981	134.8
5.00	12	111.2	1.062	145.9
	21	247.0	2.359	324.1
	33	225.2	2.150	295.4

phries and Cumming 1973; Daniel 1976; Lal et al. 1977; Rogers 1978). Larvae feeding at the estimated average field zooplankton density developed at a much slower rate.

Descriptions of the sequence and rate of utilization of the yolk and oil reserves are not consistent in the literature. Yolk and oil were resorbed simultaneously (Mansueti 1958; Doroshov 1970) or the oil persisted after total yolk absorption (Doroshov 1970; Miller 1977; Rogers 1978; this study). In no instance was the oil globule reported to persist for as long as in our study. A full discussion of the role of the oil globule is given by Eldridge, et al. (1977). We postulate that the oil functions as an energy reserve that can be conserved when food is not abundant.

The energy content of oil per unit volume is approximately double that of yolk, which makes it more practical. In the event of food deprivation, the larva can utilize this energy source rather than resorb tissue. During active feeding, oil energy and exogenous food energy both were mobilized to maximize growth. This helps to shorten the duration of the vulnerable larval life stage. This reserve could account for much of the reported resilience and adaptability of striped bass larvae (Doroshov 1970; Davies 1973; Rogers et al. 1977).

Preliminary results from the ossification and histology studies seem to indicate that differentiation in starved larvae is noticeably affected as early as 9 days after fertilization. Detailed descriptions of these processes should provide indicators that could be applied to wild larvae, as was done with northern anchovy and jack mackerel (O'Connell 1976; Theilacker 1978).

In our laboratory studies, the estimated concentration of zooplankton in the San Francisco Bay-Delta estuary (0.1 zooplankter/ml) resulted in larval survival of 51% for the feeding stage but development of the larvae was suppressed, meaning the duration of the larval stage was prolonged. Because the larval period is inherently one of high mortality, extending its duration increases mortality. Growth of our larvae feeding at the high rations approximated that of wild larvae; yet there was up to a 50-fold difference in food densities. This discrepancy may not be as divergent after we compare computed rations of wild larvae with our results, and also consider that our laboratory larvae did not have a constant density throughout a day. Nonetheless, the apparent need of striped bass larvae for food densities greater than 0.1 organism/ml in order to attain normal growth rates leads us to suggest that wild zooplankton densities may be underestimated. Zooplankton estimates are spatially integrated and provide no information on the degree of patchiness. We hypothesize that wild larvae locate patches of zooplankters denser than 0.1 zooplankter/ml, and thereby find food to meet their metabolic requirements. In similar fashion northern anchovies are believed to associate with zooplankton patches (Hunter and Thomas 1974; Lasker 1975).

Acknowledgments

We extend special thanks to the employees of the California Department of Fish and Game, Bay-Delta Fishery Project, and of the Central Valleys Hatchery for their cooperation and support of our research.

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Atlantic Skipjack Tuna: Influences of Mean Environmental Conditions on Their Vulnerability to Surface Fishing Gear

R. H. EVANS, D. R. McLAIN, and R. A. BAUER

Introduction

Of those tunas which are exploited commercially in the Atlantic, only the skipjack tuna, *Katsuwonus pelamis,* appears presently exploited at a level below that corresponding to maximum sustainable yield (Matsumoto, 1974). As a result, further increases in fishing effort by the international fleet may logically be directed toward this species. Realization of an economic return from such increased effort is complicated by the fact that the skipjack tuna is a fast swimming, wide ranging species (Kearney, 1976) which inhabits much of the tropical and subtropical Atlantic. Its availability by area and time varies greatly and it is only under certain conditions that skipjack tuna are sufficiently concentrated for economic harvest by surface gear (troll, pole and line, and purse seine).

Researchers and fishermen alike have long sought to improve the harvest of skipjack tuna by attempting to identify areas of high concentration. For fishermen this effort has taken the form of increased scouting activity over larger and larger areas. For researchers it includes identifying those areas where skipjack tuna forage is plentiful (Brandhorst, 1958; Blackburn and Laurs, 1972), ascertaining migration patterns of skipjack tuna (Rothschild, 1965; Fink and Bayliff, 1970; Williams, 1972), and defining preferred skipjack tuna habitat or habitat constraints as inferred from physical environmental indicators (Ingham, 1970; Ingham et al., 1977; Barkley et al., 1978; Sharp, 1979).

The approach of using physical environmental indicators to infer habitat limits of skipjack tuna appears preferable to habitat forecasts based on skipjack tuna forage or migration patterns because of the limited data available to assess these factors. In contrast, a comparatively large amount of physical oceanographic data is available for comparison with catch statistics since oceanographic observations are routinely made for other purposes.

Physiological experiments on captive skipjack tuna from the Pacific have been carried out to ascertain habitat preference as functions of several environmental indicators (Dizon, 1977; Dizon et al., 1977, 1978). No attempt has been made to integrate existing environment/habitat relationships and data with Atlantic catch data to define those areas where skipjack tuna should be available to surface gear. This paper attempts to do this and, in doing so, to develop working hypotheses for identifying areas of potential skipjack tuna concentration as an aid to exploiting and managing the resource.

ABSTRACT—Pertinent data and literature are examined to determine the effects of the environment on the spatial distribution of skipjack tuna, Katsuwonus pelamis, *in both the Atlantic and Pacific Oceans. Environment/skipjack distribution relationships derived from this information are applied to long-term annual mean distributions of dissolved oxygen and thermal structure for the Atlantic Ocean between lat. 40°N and 40°S. The depth of skipjack habitat is mapped. Within the defined habitat areas, high vulnerability of skipjack tuna to surface gear is inferred and areally compared with the long-term catch of the FIS (French, Ivory Coast, and Senegalese) fleet to confirm the validity of this approach. This technique is then used to hypothesize areas of vulnerability of skipjack to surface gear outside the range of the FIS fleet effort in the western Atlantic. Finally, the effects of surface winds on fishing operations are discussed and those areas where wind speed may hamper operations are outlined for the Atlantic Ocean between lat. 30°N and 30°S.*

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Environmental Constraints on Habitat

Temperature

Through the years researchers have attempted to use environmental parameters to define the distribution limits of skipjack tuna or to infer skipjack tuna-preferred habitat areas. Data on water temperature and most notably sea surface temperature has received greatest attention. Both Blackburn (1965) and Nakamura (1969) indicated that distribution limits for skipjack tuna can be defined using sea surface temperature. Laevastu and Rosa (1963) indicated worldwide occurrence of skipjack tuna is confined to the 17°-28°C range and that major skipjack tuna fisheries are found in the 19°-23°C range. More recently, Williams (1970) stated that adult eastern tropical Pacific skipjack tuna are most numerous at sea surface temperatures between 20° and 29°C. Miller and Evans[1] found that for 86 successful purse seine sets made on skipjack tuna in the eastern tropical Pacific, sea surface temperatures ranged from less than 20° to 30°C, with a pronounced mode at about 28.4°C (Fig. 1). Barkley et al. (1978) drew upon test data for captive skipjack tuna presented in Neill et al. (1976) and Dizon et al. (1977) to hypothesize that the habitat of Pacific skipjack tuna is confined to water temperatures equal to or greater than 18°C.

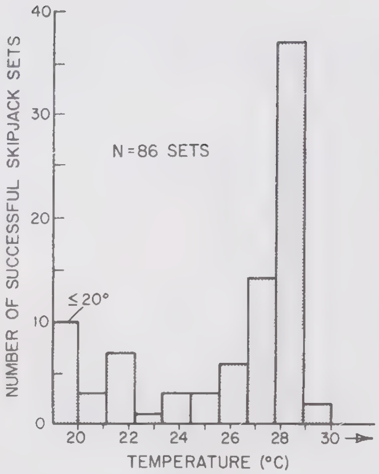

Figure 1.—Distribution of successful eastern tropical Pacific purse seine sets on skipjack tuna as a function of sea surface temperature (from Miller and Evans, footnote 1).

Another temperature related parameter which has been used to define skipjack tuna habitat limits is the depth of the isothermal or mixed layer. Green (1967) related the depth of the eastern tropical Pacific mixed layer to tuna purse seining success (Fig. 2A). Blackburn and Williams (1975) indicated that areas of high apparent skipjack tuna abundance in the eastern tropical Pacific are limited to areas where the mixed layer is less than 40 m deep. Miller and Evans (footnote 1) have examined the depth of the mixed layer and find that successful eastern tropical Pacific skipjack tuna sets are limited to mixed-layer depths of less than 85 m. Their findings show a pronounced mode for purse seine set success at 15 m (Fig. 2B) as well as a relation between skipjack tuna purse seine success and thermocline gradient (not shown).

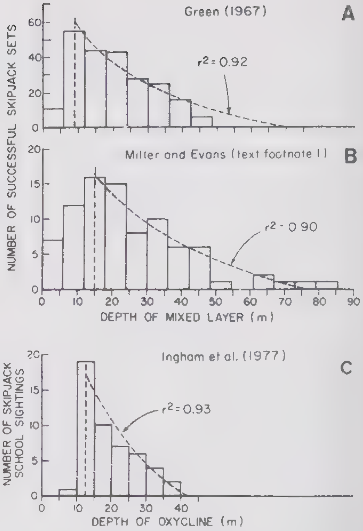

Figure 2.—Distribution of skipjack tuna school sightings and numbers of successful skipjack tuna purse seine sets as functions of the depths of the oxycline and mixed layer, respectively. A log curve has been fitted to the intervalized data to the right of the mode in each case.

Dissolved Oxygen and Salinity

Dissolved oxygen concentration has also been used to define skipjack tuna habitat. Barkley et al. (1978) have drawn on the work of other researchers to propose 3.5 ml/l as the minimum concentration of dissolved oxygen routinely tolerated by Pacific skipjack tuna. Ingham et al. (1977) found the depth of the 3.5 ml/l oxygen surface in the eastern Atlantic was related to surface skipjack tuna school sightings (Fig. 2C). Dizon (1977) indicated that captive skipjack tuna do not respond to rather drastic changes in salinity, but York (1969) has used salinity with some success in New Zealand as an "indicator" of areas of increased skipjack tuna availability. The increase in availability found by York is probably due to the presence of ocean fronts and/or convergence zones as indicated by variations in the distribution of salinity rather than by direct effects of salinity on the behavior of skipjack tuna.

Forage

Forage of skipjack tuna has been examined relative to skipjack tuna abundance. Dragovich (1970) examined the stomach contents of skipjack tuna caught by pole and line, longline, trolling, and purse seine in the eastern and western tropical Atlantic. Blackburn and Laurs (1972) used data collected during the EASTROPAC (Eastern

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[1] Miller, F. R., and R. H. Evans. The ocean environment of the eastern tropical Pacific as related to tuna purse seining. In prep.

Tropical Pacific) experiment to map the distribution of skipjack tuna forage in the eastern tropical Pacific. Blackburn and Williams (1975) found eastern tropical Pacific skipjack tuna distribution correlated with the nighttime concentration of skipjack tuna forage.

Weather

The marine environment can affect the efficiency of the fishing operation and, as a result, skipjack tuna vulnerability. Yuen (1959) indicated that cloudiness is correlated with the ability of fishermen to spot surface or near-surface skipjack tuna schools. Miller and Evans (footnote 1) found purse seine operations severely hampered when wind speed exceeds 8 m/second, with no successful sets made where wind speeds exceed 11 m/second (Fig. 3).

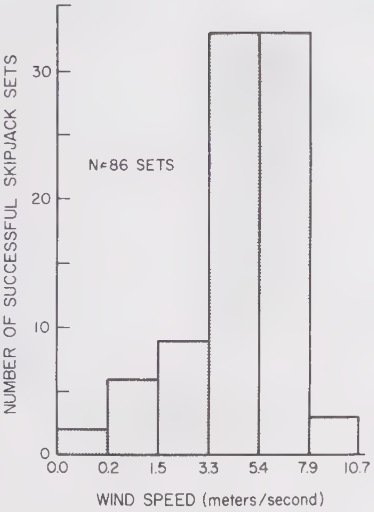

Figure 3.—Distribution of successful eastern tropical Pacific purse seine sets on skipjack tuna as a function of wind speed (from Miller and Evans, footnote 1).

Data Processing and Analysis

An examination of the methods used by previous researchers and the availability of pertinent Atlantic environmental data indicates that the approach taken by Barkley et al. (1978) is well suited to defining skipjack tuna habitat over large areas. Their method, developed from work done on Pacific skipjack tuna, uses the shallower of either the 18°C isotherm or the 3.5 ml/l dissolved oxygen surface as the skipjack tuna habitat lower boundary. Since Ingham et al. (1977) have used the 3.5 ml/l depth with success to define Atlantic skipjack tuna habitat limits, it was felt that this concentration was appropriate. Using only the depth of the 18°C isotherm as per Barkley et al. (1978), presents a problem as water temperature tolerance by skipjack tuna is size specific. They stated that all skipjack tuna have a lower boundary of 18°C but that the upper boundary for 40 cm (1.15 kg) fish is about 29°C while the upper boundary for 70 cm (7.34 kg) fish is about 23°C. Since 40 cm skipjack tuna are the smallest animals consistently taken in western Atlantic commercial catches (Coan, 1976), it was decided to set upper and lower thermal habitat boundaries for this study at 29° and 18°C, respectively. Since the sea surface temperature in this study is almost always less than 29°C (Fig. 4), this means the habitat of skipjack tuna would extend from the sea surface to the depth of either the 18°C isotherm or the 3.5 ml/l surface, whichever is shallower.

Data utilized herein were collected from a number of sources. Sea surface temperature contours were prepared from surface synoptic marine weather data, archived by the Fleet Numerical Oceanography Center (FNOC), Monterey, Calif. To prepare these data for analysis, sea surface temperature values for the period March 1971 to March 1979 were extracted, edited, checked for errors, and averaged by month and 1° square for the Atlantic Ocean between lat. 40°N and 40°S. An annual mean field for the same area was then created by taking the mean of the 12 monthly means for each 1° square. This annual mean sea surface temperature field was then computer smoothed and contoured (Fig. 5).

The depth of the 18°C isotherm was computed from data in two data files: 1) The Bauer-Robinson Numerical Atlas data file[2], File A, and 2) the National Oceanographic Data Center (NODC) station data format two (SD2) file (NODC, 1973), File B. File A for the Atlantic north of lat. 5°S contained water temperature data derived from all available mechanical bathythermograph, expendable bathythermograph, and hydrocasts taken prior to 1976. These data were organized by 1° square averages, by month, for water temperature, tabulated at 30 m intervals from the sea surface to 150 m. Below 150 m, File A contained data summarized at standard hydrocast levels. For each 1° square in File A, the mean depth of the 18°C isotherm was calculated using linear interpolation between the tabulated data points.

For areas south of lat. 5°S, File B, containing unsummarized hydrocast data, was used. For each File B hydrocast, the depth of the 18°C isotherm was computed by linear interpolation between observed levels. These values were then summarized by 1° square and month. The two mean fields derived from Files A and B were then merged and treated as was sea surface temperature to create an annual mean contour plot of the depth of the 18° C isotherm (Fig. 6).

The depth of the 3.5 ml/l dissolved oxygen surface was extracted from File B for the area in the Atlantic Ocean between lat. 40°N and 40°S using linear interpolation methods similar to those used to

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[2] Made available by Compass Systems, Inc., San Diego, Calif. Mention of trade names or commercial firms does not imply endorsement by the National Marine Fisheries Service, NOAA.

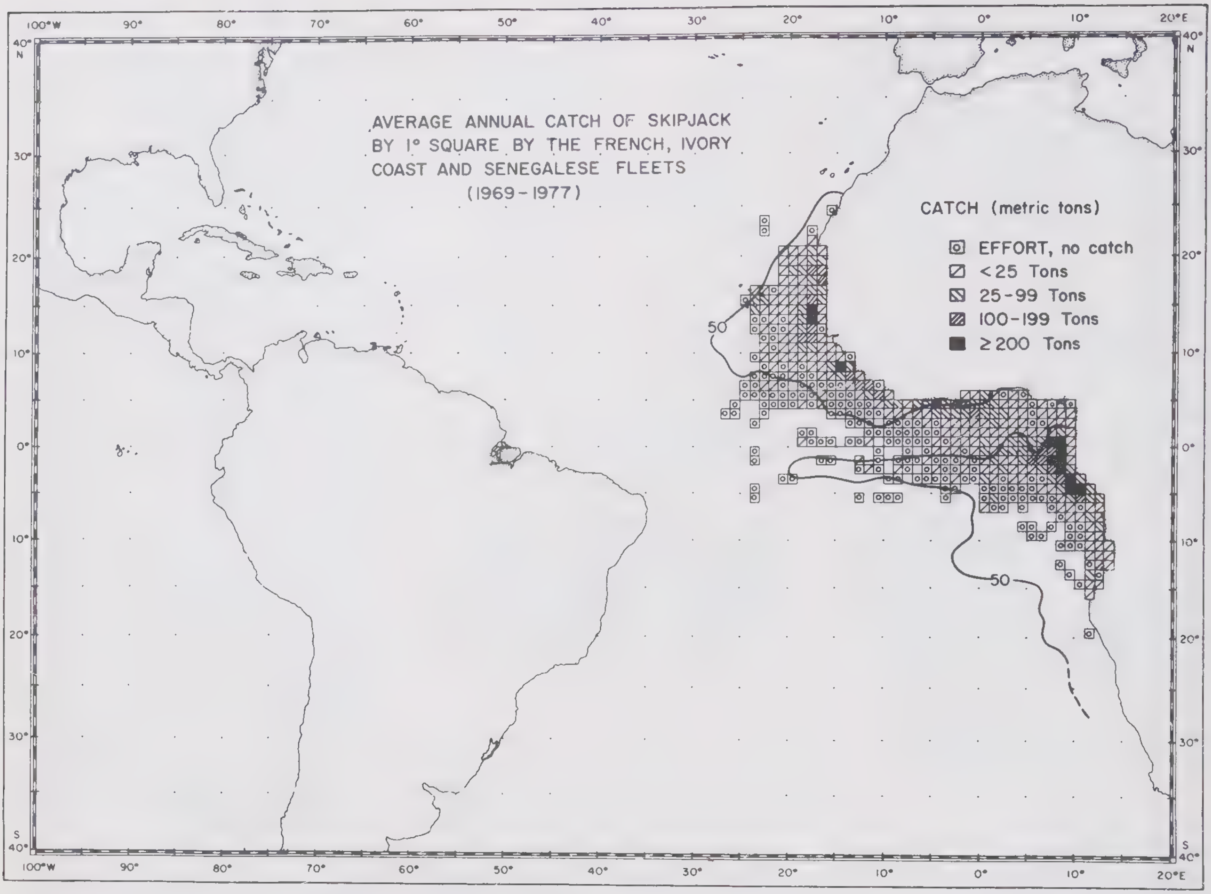

Figure 4.—Distribution of average annual catch of skipjack tuna by 1° square by the French, Ivory Coast, and Senegalese fleets (1969-77). The 50 m skipjack tuna habitat depth contour has been superimposed.

extract the 18°C isotherm (Fig. 7).

Contours of skipjack tuna habitat depth (Fig. 8) were created by analyzing a data field derived from graphically integrating the depths of the 18°C isotherm (Fig. 6) and the 3.5 ml/l dissolved oxygen surface (Fig. 7). Mean total catch in metric tons (t) by 1° square for the French, Ivory Coast, and Senegalese (FIS) fleet were extracted from ICCAT (International Commission for the Conservation of Atlantic Tunas) data bases for 1969 through 1977 (Fig. 4). These data were summed for all years, averaged, and plotted by 1° square. Those areas where fishing effort occurred in any year but where no catch was recorded were so noted.

Contours of surface, vector, mean wind speed were extracted from monthly contour plots in Hastenrath and Lamb (1977). Annual mean wind speed for the area lat. 30°N to 30°S in the Atlantic was obtained from their data by plotting monthly isotachs and then abstracting an envelope which contained all 12 monthly wind speed contours (Fig. 9). The contours presented are therefore not contours of mean wind speed but are annual, areal, composite ranges of the individual vector, mean wind speeds. Vector mean wind speed values equal to or greater than the contour value would be expected within all areas encompassed by a particular isotach (Fig. 9) at some time during the year but not necessarily during all months.

Discussion

Traditionally, surface fisheries for Atlantic skipjack tuna have been largely confined to eastern tropical areas for which representative catch-effort data are available. No such time series of catch-effort data exists for the more localized fishing areas of the western Atlantic and an alternate method of identifying

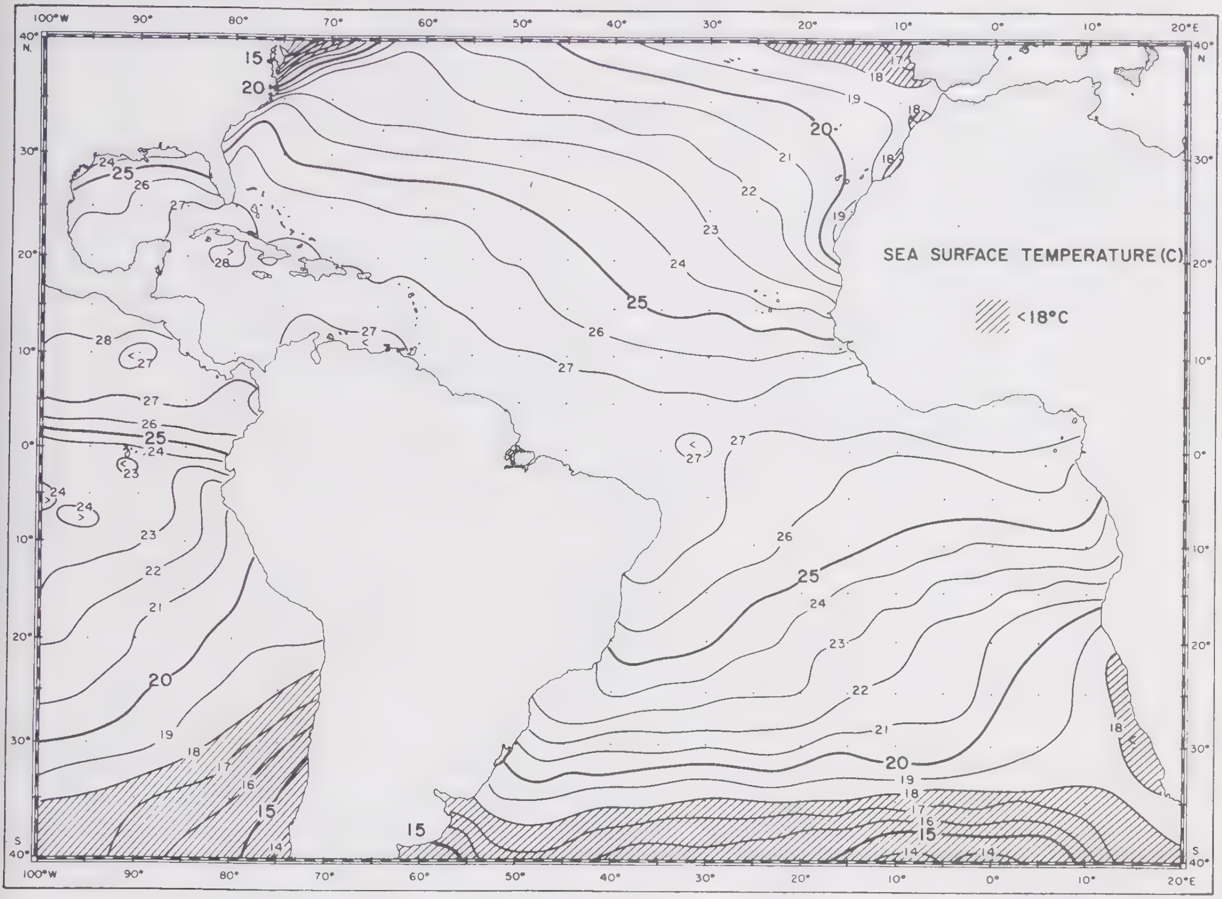

Figure 5.—Long-term annual mean sea surface temperature field, 1971-79. Hatched areas are colder than 18°C.

probable areas of skipjack tuna availability is required. Such an approach would be to identify areas suitable for skipjack tuna habitation. Previously described criteria of Barkley et al. (1978) (those regions confined within the 3.5 ml/l and 18°C surfaces) were used to define areas suitable for skipjack tuna habitation in the Atlantic between lat. 40°N and 40°S.

In using the 18°C isotherm as a lower thermal boundary for skipjack tuna habitat, there are some areas of the Atlantic where the entire water column is colder than this value. Those areas, which are shown to contain no skipjack tuna habitat, are readily apparent in the sea surface temperature field (Fig. 5). They include: 1) Almost all of the Atlantic south of lat. 34°S, 2) the area of strong upwelling of cold waters along the coast of southwest Africa between lat. 20°S and 34°S, 3) two smaller upwelling areas off the northwest coast of Africa, 4) the water northwest of Portugal, and 5) the waters off the east coast of the United States north of the Gulf Stream.

Remaining areas having surface temperatures in excess of 18°C are potential skipjack tuna habitat areas. Examination of habitat depth as defined by 18°C isotherm (Fig. 6) shows habitat depth is shallowest in the eastern Atlantic, increasing gradually toward two depth maxima located near the centers of the subtropical gyres in the north and south Atlantic. These areas of maximum thermal habitat depth are separated by a ridge of shallower depth located between the Equator and lat. 10°N caused by equatorial upwelling. Several of the areas of shallowest thermal habitat off northwest and southwest Africa and the area off the south coast of Brazil are coincident with areas of coastal upwelling.

Depth contours of the 3.5 ml/l dissolved oxygen surface (Fig. 7),

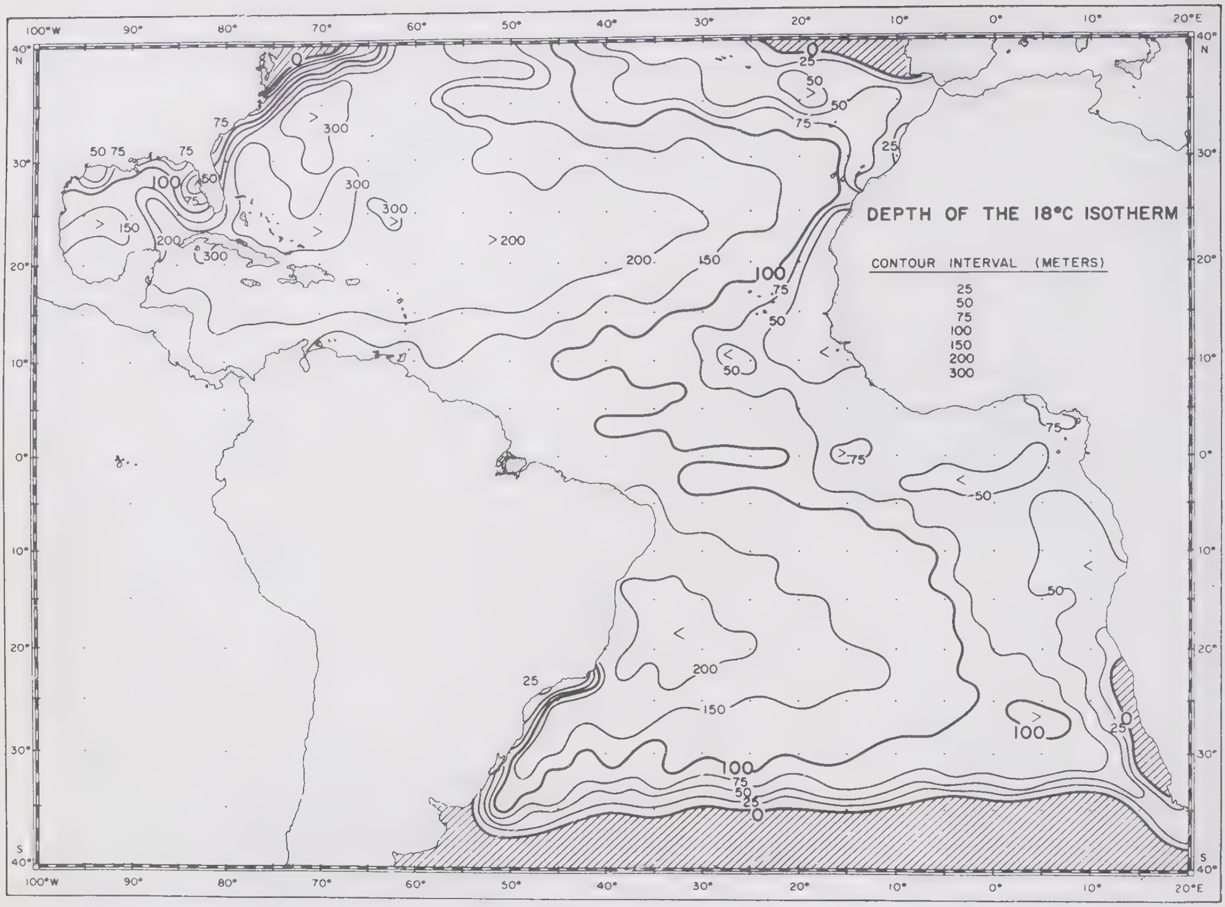

Figure 6.—Long-term annual mean depth of the 18°C isotherm. Hatched areas are colder than 18°C at all depths.

the second habitat constraining parameter, display similar large-scale features. As with the depth of the 18°C isotherm, the 3.5 ml/l surface is shallow in the eastern Atlantic, becoming deeper to the west. This layer also deepens poleward from the tropics due to higher dissolved oxygen capacity of colder water. A trough in the 3.5 ml/l surface symmetric about the Equator appears to be associated with the equatorial undercurrent. As with the 18°C isotherm, coastal upwelling causes shoaling of the 3.5 ml/l surface in the areas off southwest and northwest Africa and southern Brazil. For the areas off Argentina, northern Brazil, and Venezuela, shoaling of the 3.5 ml/l surface may not be caused by upwelling in the immediate area but rather by an increase in primary productivity associated with the advection of upwelled waters out of the source area[3].

In nearshore areas high rates of primary production associated with upwelled waters inhibit light penetration. This causes a decrease in the compensation depth which in turn causes a shoaling of the near surface dissolved oxygen maximum (footnote 3) and the 3.5 ml/l surface. Advection of surface waters, and to some extent turbulent mixing, may transport nutrient-rich surface water out of the upwelling area. An example of this would be the shoal area (less than 50 m) of the 3.5 ml/l surface extending into the Atlantic from the coast of Brazil near lat. 20°S. Mascarenhas et al. (1971) indicated significant coastal upwelling as well as large cyclonic and anticyclonic eddies in this area. These findings agree with those of Reid et al. (1977) who stated that a substantial poleward flow exists just offshore of the Brazil current. These mechanisms could combine to advect substantial quantities of nutrient-rich surface water, off-

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[3] See pages 85-86 in Parsons and Takahashi (1973).

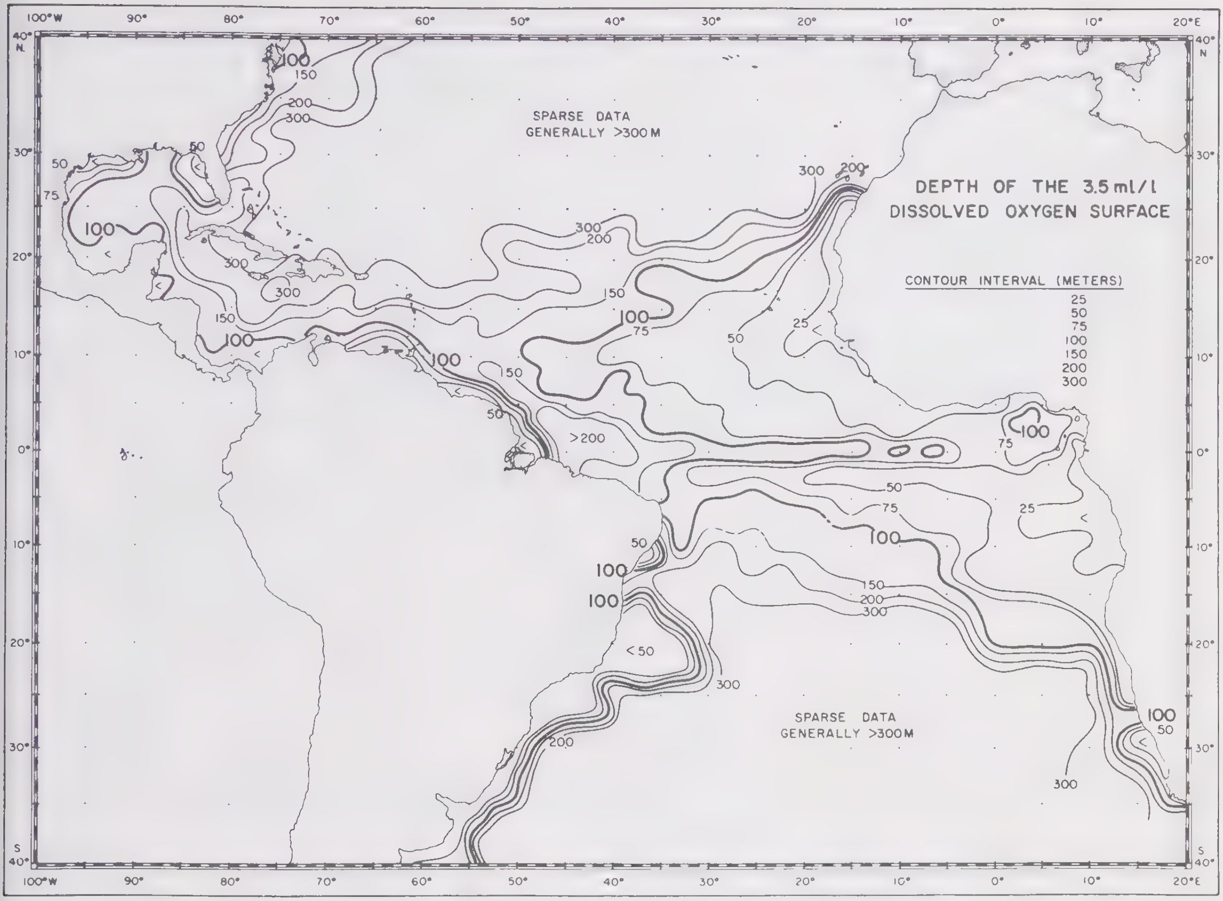

Figure 7.—Long-term annual mean depth of the 3.5 ml/l dissolved oxygen surface.

shore and equatorward in the area in question, thereby creating features in the 3.5 ml/l contours that are not consistent with or observed in the contours for the depth of the 18°C isotherm or sea surface temperature.

Figure 8 depicts the areal depth of skipjack tuna habitat indicating that skipjack tuna are capable of inhabiting almost all of the Atlantic between lat. 40°N and 34°S. Except for areas influenced by coastal upwelling, habitat depth is controlled by the depth of the 18°C surface poleward of about 15° latitude in either hemisphere. In the equatorial band (between lat. 15°N and 15°S), habitat depth is determined by dissolved oxygen concentration.

Having established that skipjack tuna can inhabit portions of the water column in most of the Atlantic between lat. 40°N and 34°S, it is necessary to define and limit those areas where skipjack tuna may be vulnerable to surface fishing gear. It seems reasonable that skipjack would be most vulnerable in those areas where their habitat is restricted to the near-surface layer. This is suggested by each of the panels in Figure 2. Figures 2A and 2B depict results of eastern tropical Pacific studies relating skipjack tuna purse seine success to the depth of the mixed (isothermal) layer. Both Figures 2A (Green, 1967) and 2B (Miller and Evans, footnote 1) utilize eastern tropical Pacific skipjack tuna purse seine data from the early 1960's and 1970's, respectively. Figure 2C (Ingham et al., 1977) compares Atlantic research ship sightings of surface skipjack tuna schools to oxycline depth.

Catch/school sighting trends with depth are remarkably similar in each panel. At depths shallower than the "critical depth" (defined as the mode of each of the distributions in Figure 2), catch and school sightings drop off markedly. At depths greater than the "critical depth," catch and school sightings drop off more slowly and in an exponential fashion as is indicated by the log

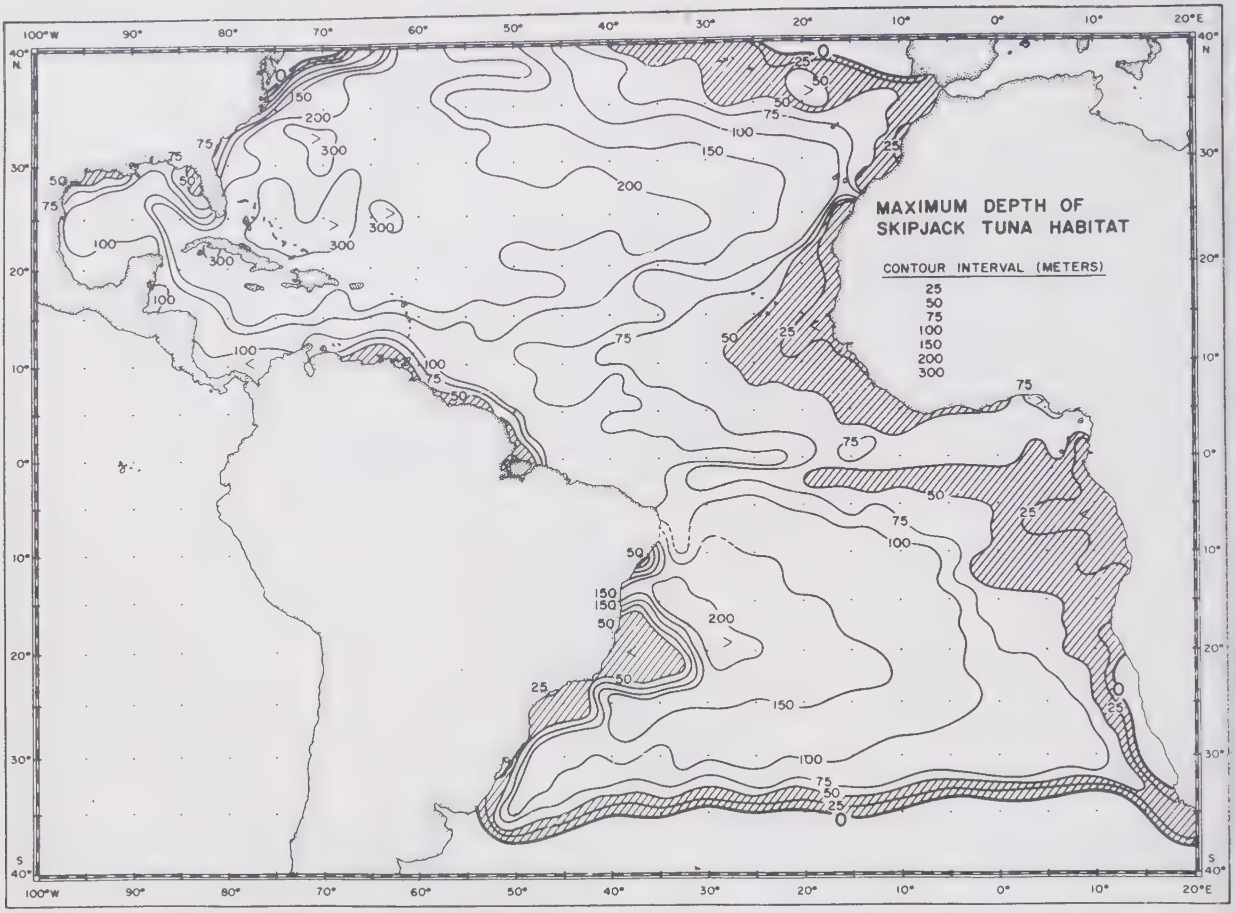

Figure 8.—Annual mean contours of maximum depth of skipjack tuna habitat, derived from graphical integration of Figures 6 and 7. Hatched areas indicate depths less than 50 m.

curve which has been fitted in each case. This suggests that skipjack tuna are less vulnerable in areas where the habitat depth is shallower than the critical depth (10-15 m). Decreased vulnerability in these shallow layers may be due to avoidance of such a constrained environment for possibly habitat layers shallower than 10-15 m do not routinely exist in nature. At habitat depths deeper than 10-15 m skipjack tuna catch/school sightings fall off more slowly. This decrease in vulnerability may be due to a simple increase in habitat volume.

For all three of the studies depicted in Figure 2, catch or school sightings are zero or extremely small for mixed layer or oxycline depths deeper than 50 m. It can be reasonably concluded, therefore, that skipjack tuna are not vulnerable to surface fishing gear or detection in areas where either of these parameters exceeds 50 m depth.

To examine this hypothesis, equivalence of oxycline and mixed layer depths to the 3.5 ml/l and 18°C surfaces, respectively, must be established. In this regard, the criteria used to define the oxycline in Figure 2C is the 3.5 ml/l surface (Ingham et al., 1977). Where the lower habitat limit is the 18°C isotherm it will by definition be equal to or deeper than the mixed layer depth. Therefore, the habitat depth will be either coincident with or somewhat deeper than the oxycline or mixed layer depth. Consequently, a habitat depth of 50 m would seem a reasonable assumed limit of vulnerability of skipjack tuna to surface gear.

To test the validity of a maximum depth of vulnerability, the 50 m habitat depth contour was plotted over the catch distribution for skipjack tuna for the FIS fleet for 1969-1977 (Fig. 4). Essentially all the catch falls in areas where the habitat depth is less than 50 m. A notable exception occurs in a nar-

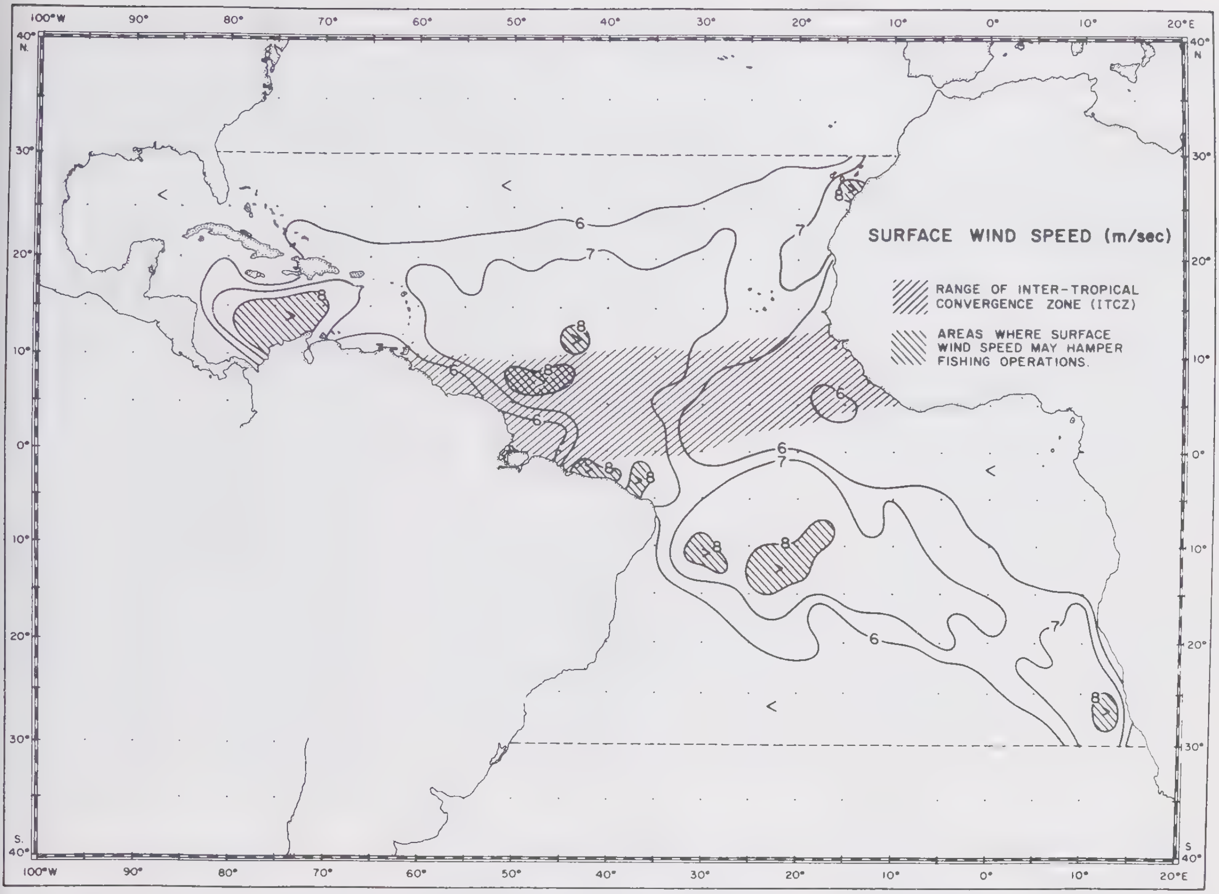
SURFACE WIND SPEED (m/sec)
RANGE OF INTER-TROPICAL CONVERGENCE ZONE (ITCZ)
AREAS WHERE SURFACE WIND SPEED MAY HAMPER FISHING OPERATIONS.
100°W
90°
80°
70°
60°
50°
40°
30°
20°
10°
0°
10°
20°E
40° N.
30°
20°
10°
0°
10°
20°
30°
S. 40°
6
7
8

Figure 9.—Long-term mean annual contours of the seasonal range of selected sea surface wind speed values (m/second). Hatching depicts those areas where the surface wind speed is equal to or greater than 8 m/second and/or the annual range of the Inter-Tropical Convergence Zone; based on convergence of the surface wind field.

row band just north of the Equator between the coast and long. 6° W where the habitat is 50-75 m deep (Fig. 8). This is an area of highly variable oceanographic conditions (Dietrich, 1963). It is possible that the habitat depth in this area is less than 50 m on a seasonal basis and that the indicated catch occurs during these periods.

A maximum depth (50 m) of vulnerability of skipjack tuna to surface gear is indicated by hatching in Figure 8. As indicated, several areas in the western Atlantic have habitat depths appropriate for skipjack tuna vulnerability to surface gear (Fig. 8) including: 1) Off Argentina and along the south coast of Brazil, 2) off Venezuela and along the north coast of Brazil, 3) along the northern half of the Gulf Stream off the United States, and 4) along a band extending northwestward from the northwest African coast.

As previously indicated, surface wind speed can seriously restrict fishing operations and thereby the catchability of skipjack tuna by surface gear. Since purse seining success falls off markedly at wind speeds above 8 m/second (Fig. 3), that value has been taken as critical and areas where wind speed may exceed that value during the year have been hatched in Figure 9. Of those areas having high wind conditions only the area off Africa at lat. 28°S is coincident with an area where the skipjack tuna habitat depth is less than 50 m.

Figure 9 also includes the annual range of position of the Inter-Tropical Convergence Zone (ITCZ); that region where easterly trade winds from the northern and southern hemispheres meet. The ITCZ is traditionally an area of alternately squally, severe weather and light winds. Fishermen purse seining for tuna in the tropical

Pacific often fish in the area of light winds found on occasion adjacent to the ITCZ.

Conclusions

Previous research demonstrates that relationships between the behavior or catch of skipjack tuna and the marine environment can be defined. An analysis of this research indicates that the depth of the 3.5 ml/l dissolved oxygen surface and the depth of the 18°C isotherm in combination provide viable constraints on skipjack habitat. Applying these constraints to existing environmental data fields yields three-dimensional representations of skipjack tuna habitat which show that: 1) Almost all of the surface layer of the Atlantic Ocean between lat. 40°N and 34°S is suitable for habitation by skipjack; 2) the habitat depth or floor is shallowest in the eastern Atlantic, becoming deeper toward the west with the deepest areas occurring at the center of the subtropical gyres in either hemisphere; 3) coastal upwelling of nutrients feeds areas of high primary production which in turn cause shoaling of the oxygen maximum layer, the 3.5 ml/l surface and the habitat floor; and 4) advection and turbulent mixing may tend to displace areas of shoaling associated with primary production away from the upwelling source area.

Definition of skipjack tuna habitat does not imply they will be vulnerable to surface fishing gear throughout their range. Previous studies suggest that skipjack tuna cease to be vulnerable to surface gear at habitat depths in excess of 50 m. This concept is tested with favorable results against the catch by surface gear of the FIS fleet and then extrapolated to the western Atlantic to determine areas of high expected vulnerability.

The areas of high potential skipjack vulnerability in the western Atlantic include: 1) The nearshore regions off the east coasts of Brazil and Argentina between lat. 16°S and 32°S, 2) the areas off the north coast of Brazil and Venezuela between long. 48°W and 68°W, and 3) the northern edge of the Gulf Stream off the east coast of the United States north of lat. 35° N.

Finally, surface wind speed is shown to hamper fishing operations with purse seine gear when the wind speed exceeds 8 m/second. Those areas where the vector mean wind speed may exceed this value seasonally are outlined and are generally found to lie outside areas of potential skipjack vulnerability.

Future Research

At this point it is appropriate to indicate that the use of annual mean oceanographic data to define skipjack habitat has certain drawbacks. Averaging over extended scales in both time and space can have the effect of: 1) Masking seasonal and spatial fluctuations in the various data fields, 2) allowing extreme values in a locale (in both time and space) to dominate annual signals, and 3) causing areas of high variability in the data fields to appear constant in space and time.

As a result, the analyses presented herein may fail to depict or sometimes misrepresent skipjack tuna habitat over small areas or where only seasonal vulnerability occurs. A case in point is that area of the Caribbean just to the west of the Lesser Antilles where turbulence from flow through the island arc and over shoal areas during March and April causes skipjack tuna to be locally vulnerable to surface gear (Ingham and Mahnken, 1966).

This does not mean, however, that the approach of using annual averaged data is invalid. On the contrary, the analyses in this paper provide an overview of conditions for the entire Atlantic. As such, they contain useful information for resource exploitation and management and aids for determining those areas to which further research addressing shorter time scales should be directed.

Acknowledgments

The authors wish to thank Margaret Robinson, Compass Systems, Inc., and Joseph Reid, Scripps Institution of Oceanography. Their considerable knowledge of archived oceanic temperature and dissolved oxygen data was an invaluable aid in analyzing the data fields presented in this paper. The efforts of Lorraine Prescott, Southwest Fisheries Center, in preparing the numerous drafts of this paper are deeply appreciated.

Note added in proof: This paper was first presented to the International Commission for the Conservation of Atlantic Tunas (ICCAT) in November 1979. In 1980 the catch of skipjack tuna by Brazil increased more than threefold to 7,000 t (ICCAT preliminary figures). All of the increased catch appears to have come from an area off southern Brazil defined by the authors as suitable skipjack habitat and an area where skipjack should be routinely vulnerable to surface fishing gear.

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RESPIRATION RATES AND LOW-OXYGEN TOLERANCE LIMITS IN SKIPJACK TUNA, *KATSUWONUS PELAMIS*

REGINALD M. GOODING,[1] WILLIAM H. NEILL,[2] AND ANDREW E. DIZON[1]

ABSTRACT

Oxygen-uptake rates and swimming speeds of voluntarily active skipjack tuna, *Katsuwonus pelamis*, at 23°-24° C were measured in the laboratory from captivity-habituated fish (0.6-3.8 kg) and at sea from just-caught fish (1.8-2.2 kg). In the shipboard tests, skipjack tuna swam 2-5 lengths/s (length = fork length) and consumed 0.9-2.5 (median = 1.3) mg O_2/g per h during their first 2.2 h of captivity. In laboratory tests, skipjack tuna swam at a mean speed of 1.4 lengths/s and consumed oxygen at a mean rate of 0.52 mg O_2/g per h. For the laboratory fish, routine swimming speed (S, in lengths/second) was inversely related to fish weight (W, in grams)—$S = 3.12 - 0.53 \log_{10} W$; oxygen-uptake rate ($\dot{V}_{O_2}$, in milligrams O_2/gram per hour) was directly related to both weight and speed (i.e., speed independent of weight effects)—$\log_{10}\dot{V}_{O_2} = -1.20 + 0.19/\log_{10}W + 0.21\ S$. However, laboratory fish swimming at their characteristic (weight dependent) speeds respired at rates independent of weight. Calculations based on the above interrelations among metabolic rate, swimming speed, and body weight indicated that skipjack tuna of all sizes may have an optimum swimming speed (for maximum distance per unit energy expenditure) near 2.1 lengths/s.

Captivity-habituated skipjack tuna (0.8-3.4 kg) also were subjected to a step decrease in concentration of dissolved oxygen (O_2) at 23°-24° C to determine their responses to acute hypoxia. At levels of O_2 below 4 mg/l, voluntary swimming speed increased as O_2 declined, reaching 3.9 lengths/s at the lowest test value of O_2, 1.4 mg/l. The 4-h median tolerance limit for low O_2 proved similar to the O_2 level critical for change in swimming speed, about 4 mg/l.

Experimental results are analyzed and compared with those from other fishes to arrive at the following conclusions: 1) The skipjack tuna's "standard" metabolic rate is two to five times that of typical fishes of similar size; 2) the weight exponent for "standard" metabolic rate of skipjack tuna is a positive value near 0.2, as opposed to the −0.2 value typical of fishes; 3) but, because the characteristic swimming speed of routinely active skipjack tuna is inversely related to weight, routine metabolic rate is virtually independent of fish weight; 4) highly active skipjack tuna can consume oxygen from air-saturated seawater at rates exceeding those known from any other fish of similar size; and 5) the skipjack tuna is relatively inefficient in its use of oxygen and food-energy for swimming (at least at low speeds) and it dies at O_2 levels still well above those lethal for other fishes.

Until the mid-1960's the environmental requirements of commercially important tunas (Scombridae) were known mainly from correlations between fishery catch rates and oceanographic conditions (see discussions by Robins 1952; Laevastu and Rosa 1963; Broadhead and Barrett 1964; Blackburn 1965; Williams 1970; Blackburn and Williams 1975; Matsumoto 1975). With the advent of techniques for studying tunas in captivity (Magnuson 1965; Nakamura 1972), many unresolved issues of tuna biology could be explored such as feeding and gut-evacuation rates (Magnuson 1969), auditory perception (Iversen 1967), visual perception (Nakamura 1968; Tamura et al. 1972), thermoperception (Dizon et al. 1974, 1976; Steffel et al. 1976), nerve-muscle physiology (Rayner and Keenan 1967), tissue metabolism (Gordon 1968), respiratory physiology (Stevens 1972), body temperature and thermal inertia (Stevens and Fry 1971; Neill et al. 1976), lethal temperatures (Dizon et al. 1977), swimming mechanics (Magnuson 1970), and swimming speed as a function of water temperature (Stevens and Fry 1971; Dizon et al. 1977), dissolved oxygen (O_2) concentration, and salinity (Dizon 1977). In addition, several works of a more integrative nature (Magnuson 1973; Barkley et al. 1978; Kitchell et al. 1978; Stevens and Neill 1978) have drawn heavily on these and unpublished laboratory studies. Among the latter are the experiments documented in this paper on oxygen-uptake rates and limits of tolerance to low oxygen in skipjack tuna, *Katsuwonus pelamis*.

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Respiration research on tunas is still quite limited. Besides the present work, there are only four published studies—three involving tuna metabolism (Gordon 1968; Stevens 1972; Brill 1979) and one involving tunas' lower tolerance limits for O_2 (Anonymous 1965). Gordon (1968), using volumetric microrespirometers, determined rates of oxygen uptake in minced preparations of muscle from skipjack tuna and bigeye tuna, *Thunnus obesus*. Stevens (1972) measured the oxygen concentration of water entering and leaving the gills of restrained, perfused skipjack tuna; from these data he computed oxygen-uptake rate and utilization. Brill (1979), using a similar technique, estimated the relation between standard metabolism and body weight of skipjack tuna. Stevens (1972) also measured oxygen utilization in free-swimming skipjack tuna by sampling exhaled water collected via opercular cannulation. Experiments conducted with skipjack tuna at the Kewalo Research Facility provided the earliest estimate of the lower lethal-oxygen limit for a tuna (Anonymous 1965).

Our purposes in this work were 1) to determine the magnitude of oxygen-uptake rate in routinely active skipjack tuna, 2) to establish the relation among oxygen-uptake rate, swimming speed, and body weight in skipjack tuna, and 3) to estimate the lowest concentration of O_2 that skipjack tuna can withstand for 4 h. The results already have contributed importantly to the development of models of skipjack tuna distribution (Barkley et al. 1978) and bioenergetics (Kitchell et al. 1978).

MATERIALS AND METHODS

Source and Preexperimental Treatment of Fish for Laboratory Experiments

Skipjack tuna were caught by angling in Hawaiian waters at sea-surface temperatures between 23° and 24° C. The fish were transported in 2,400 l shipboard tanks that were supplied with flowing seawater and supplemental oxygen. Upon arrival at the National Marine Fisheries Service's Kewalo Research Facility in Honolulu, the skipjack tuna were transferred into either 40,000 or 700,000 l outdoor holding tanks. Nakamura (1972) described in greater detail the techniques that have been developed at the Kewalo Research Facility for transporting and maintaining live tunas.

The seawater in the holding tanks had 23°-24° C temperatures, pH 7.4-7.6, 32-33‰ salinity, and 6.4-6.7 mg/l O_2. The seawater well that supplied water to the holding tanks was also the source of water for the experimental tanks. At night the holding tanks were illuminated at a low level.

Experiments were conducted with fish that had been in captivity 7-26 d. Once the skipjack tuna started feeding (usually within 3-5 d after capture), they were fed to satiation on thawed northern anchovies, *Engraulis mordax*, or smelt, *Allosmerus* sp., once a day. Prior to experiments, the fish were fasted for periods ranging from 24 to 27 h, which is more than sufficient time for gut evacuation in skipjack tuna (Magnuson 1969). However, our method of moving fish from the holding to the experimental tanks involved some food ingestion. Two to four hours before data collection, the fish were removed from a holding tank by angling with a baited, barbless hook. Although a small piece of food (1-2 g) was usually swallowed, this transfer technique did select healthy and actively feeding fish.

Oxygen-Uptake Experiments in Laboratory

Apparatus

Two unstirred, sealed respirometers of different sizes were used. Circulation of water during experiments was provided only by movements of the fish.

The larger respirometer was used only during the first of the 10 series of experiments (Table 1). The circular chamber was a vinyl-lined plywood tank, 4.57 m in diameter and 1 m deep, with a cover made of transparent vinyl film bonded to an inflatable tube, 18 cm in cross section, that encircled the tank's inner perimeter just below the rim. After the tube was in place and any trapped air had been removed with an electric pump, the clear plastic cover lay over the entire water surface, forming an effective seal. We initially had intended to run all of the experiments with this respirometer. However, it proved to be difficult to operate and visibility of fish within the chamber was poor. Most importantly, a tank of its volume (16,000 l) required a large biomass of fish in each experiment to effect oxygen reduction in a reasonably short period of time. Skipjack tuna are difficult and expensive to capture and maintain; so, to use fish as economically as possible, we built a smaller respirometer for the nine subsequent series of experiments.

The smaller respirometer consisted of a fiber glass tank, elliptical in the horizontal plane; it held 2,400 l of water and was 2.44 m long by 1.83 m wide by 0.61 m deep (Figure 1). The top edge of the tank had a 5.0 cm wide lip to which was cemented a 0.9 cm thick sponge-neoprene gasket; on this gasketed lip, there was seated, and firmly clamped, a rigid cover made of 0.4 cm thick transparent acrylic plastic strengthened by three 10 cm wide strips of 6.5 cm thick marine plywood cemented to its outer surface. A short length of 5 cm PVC pipe, which served as a vent and access port, was tapped vertically through the plastic and plywood in the center of the cover. Glued flush with the inside surface of the acrylic, the pipe extended about 8 cm above the water level.

An inlet and drain allowed fresh seawater to flow through the chamber at rates up to 190 l/min. Both inlet and drain were valved. By slightly overfilling the chamber before closing the inlet valve, we caused the acrylic cover to bulge upward 4 cm at the center. The domed conformation permitted the easy removal of bubbles from the chamber through the vent pipe. A sponge rubber ball, fitted snugly into the pipe during experiments, completed the seal.

Both respirometers were illuminated with overhead fluorescent lights. Indirect natural light coming through windows and doors was not excluded. Visibility of fish in the smaller respirometer was excellent, permitting detailed observation of fish speed and behavior during an experiment.

Dissolved oxygen measurements in both respirometers were made with a YSI[3] model 51A oxygen-temperature meter coupled with a YSI model 5418 oxygen-temperature probe. For measurements in the larger respirometer, water was electrically pumped between the tank and a small acrylic chamber in which the probe was mounted. In experiments involving the smaller respirometer, the oxygen-temperature probe was placed inside the tank through the vent pipe in the cover. The probe was vigorously jiggled for about 15 s before each reading of the meter; during the intervals between readings, a sponge rubber ball

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[3] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA, or by Texas A&M University.

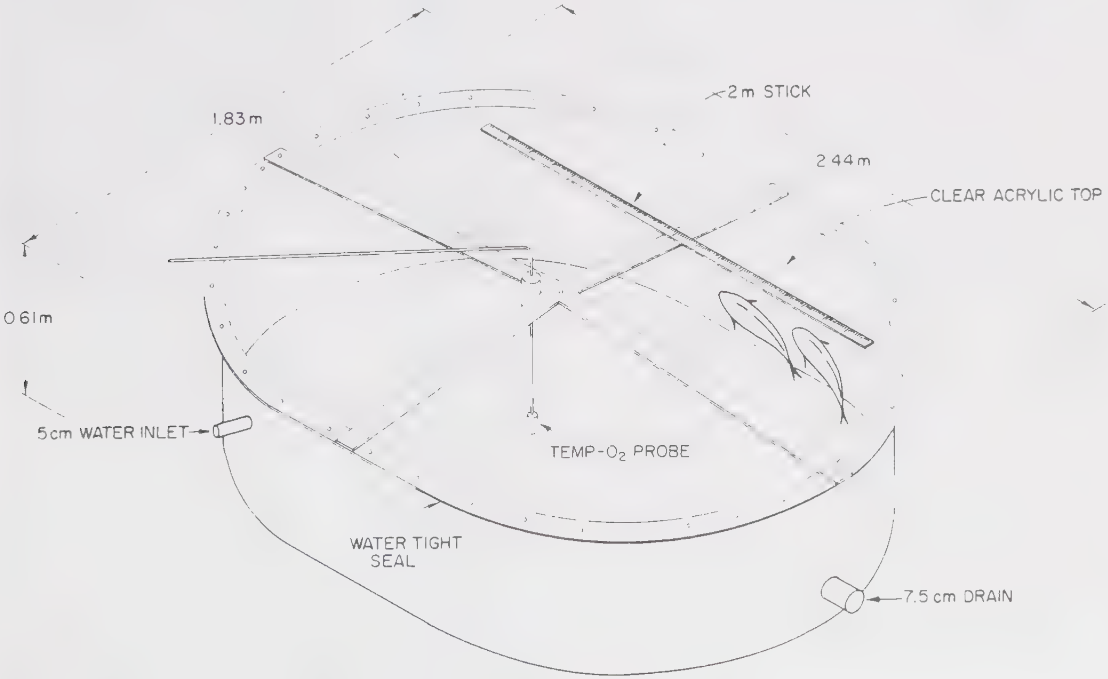

FIGURE 1.—The small sized respirometer used in oxygen-uptake experiments 2-10 on skipjack tuna

was seated tightly against the cable connecting probe and meter. Calibration of the O_2 meter was checked against air-saturated seawater at the start, midpoint, and end of each experimental run; and the temperature readings were frequently verified with a mercury thermometer. As an additional check on the O_2 meter's accuracy, readings were twice compared with Winkler determinations. The instrument gave stable and reliable readings with accuracy ±0.2 mg O_2/l.

Oxygen was supplied from standard 6,800 l cylinders through fine (800 grit) 15 cm aluminum oxide grinding stones (Baldwin 1970) to produce minute bubbles.

Preliminary and Control Experiments

Preliminary experiments conducted in each respirometer and subsequent work by Dizon (1977) indicated that skipjack tuna demonstrate no overt behavioral manifestations of stress as long as O_2 levels are maintained above 4.5 mg O_2/l. We thus assumed that the fish under our experimental conditions would exhibit respiratory independence between 7.0 and 5.0 mg O_2/l. All subsequent oxygen-uptake experiments were conducted within that range.

The preliminary experiments indicated that 1.5-2.0 g of fish per liter of water consumed oxygen at a rate that would limit a run to <3 h, which we rather arbitrarily set as about the maximum time an experiment should last.

Experimental Procedure

The 10 series of 4 experiments each were made with groups of 2-8 fish (Table 1). The basic procedures for a series of experimental runs were essentially the same for both respirometers. The detailed procedures, herein described, are for experiments with the small respirometer.

Each series of experimental runs started between 0900 and 1100 h and continued through the day and night, into the early hours of the follow-

TABLE 1.—Respiration rate experiments with laboratory held skipjack tuna. Length measure is fork length.

Fish lot	Number of fish	Mean weight and range (g)	Mean length and range (cm)	Experiment	Respiration rate (mg O_2/g per h)	Mean respiration rate of fish lot	Swimming speed (*L*/s)	Mean swimming speed
1	8	3,834 (3,114-5,222)	58.6 (53.2-68.0)	1	0.561	0.499	1.2	1.1
				2	0.485		1.1	
				3	0.408		0.9	
				4	0.542		1.1	
2	6	671 (530-844)	36.1 (33.3-39.0)	1	0.488	0.551	1.7	1.7
				2	0.590		1.8	
				3	0.532		1.8	
				4	0.600		1.7	
3	5	632 (475-805)	35.5 (31.5-38.1)	1	0.581	0.506	2.2	1.8
				2	0.542		1.9	
				3	0.462		1.7	
				4	0.439		1.5	
4	2	1,719 (1,412-2,026)	44.8 (42.4-47.2)	1	0.525	0.522	1.5	1.4
				2	0.560		1.3	
				3	0.476		1.5	
				4	0.529		1.2	
5	2	2,539 (2,411-2,667)	52.8 (52.7-52.8)	1	0.456	0.382	1.2	1.2
				2	0.364		1.2	
				3	0.360		1.2	
				4	0.350		1.3	
6	2	1,703 (1,496-1,910)	45.1 (43.5-46.7)	1	0.578	0.555	1.8	1.6
				2	0.561		1.6	
				3	0.520		1.5	
				4	0.564		1.6	
7	2	2,178 (1,890-2,467)	49.3 (47.1-51.5)	1	0.574	0.577	1.2	1.4
				2	0.576		1.6	
				3	0.577		1.6	
				4	0.581		1.3	
8	2	2,790 (2,523-3,057)	51.6 (49.8-53.3)	1	0.778	0.658	1.7	1.4
				2	0.624		1.1	
				3	0.624		1.3	
				4	0.608		1.3	
9	2	1,349 (1,161-1,537)	44.6 (42.4-46.7)	1	0.395	0.395	1.2	1.3
				2	0.346		1.1	
				3	0.404		1.9	
				4	0.434		1.1	
10	2	2,200 (2,132-2,268)	50.2 (48.3-52.1)	1	0.580	0.575	1.3	1.3
				2	0.565		1.3	
				3	0.563		1.2	
				4	0.593		1.4	
Overall means		1,962	46.9		0.522			1.4

ing morning. The skipjack tuna were transferred from the holding tank to the respiration tank through which water was flowing at about 130 l/min. The fish were observed for 30 min and any that showed unusual behavior was replaced with another fish from the holding tank. Then the cover of the respirometer was installed and the water flow, now supplemented with oxygen, was continued. The animals were allowed to habituate until they were schooling and swimming slowly around the chamber at about 1.5 fork lengths/s (*L*/s) with no overt signs of stress. During this period (1-3 h) O_2 concentration in the chamber was maintained at air saturation, 6.9-7.0 mg O_2/l. The outlet water valve was then closed, the oxygen shut off, and the inflowing water was reduced to about 10 l/min. The chamber was slowly filled with water until the acrylic cover domed; then the inflow of water was stopped. When all bubbles were excluded, the sponge rubber ball was positioned to seal the vent pipe and the first experimental run was begun. At the start of a run, O_2 concentration in the respirometer was between 6.9 and 7.0 mg O_2/l. Oxygen concentration, temperature, swimming speed, and general behavior of the fish were monitored and recorded every 15 min. Swimming speed was estimated by measuring the mean time for three passes by the fish over a straight line distance of 1-2 m. (A comparison of values obtained from this technique with mean speeds during complete circuits of fish in the respirometer showed that speed was essentially constant and that the technique yielded an accurate measure of mean speed during a given circuit.) When the O_2 level in the respirometer had been reduced to 5.0 ± 0.1 mg O_2/l, final observations were recorded and the run terminated.

A water flow of about 130 l/min and oxygenation were then resumed, which quickly brought the O_2 in the respirometer up to about 7.0 mg O_2/l where it was maintained for from 1 to 1.5 h until the start of the next run. Following the same procedure, three more runs were made with each group of fish. In all of the experiments, the fish appeared to be in as good condition at the end of a four-run series as they had been at the beginning.

Oxygen Consumption by Just-Caught Skipjack Tuna

Rates of oxygen uptake were measured in 11 tank-lots of skipjack tuna while they were in shipboard transit between the fishing grounds and the shoreside research facility in Honolulu. These observations were made during three separate fishing trips during December 1972 (*Charles H. Gilbert* cruise 129). Sea-surface temperature was uniformly 24° C.

Apparatus

The five transport tanks served as respirometers. Except for the type of cover and differences in plumbing, these tanks were almost identical to the smaller laboratory respirometer described above. The cover of each transport tank consisted of an elliptical fiber glass plate with an open hatchway in its center (see fig. 15 in Nakamura 1972). The hatchway was an 80 by 48 cm oval in cross section and extended, chimneylike, 20 cm above the plane of the tank cover. Each cover was tightly bolted to the gasketed rim of its tank.

Seawater was pumped through each tank at a nearly constant rate between 150 and 250 l/min. Water entered a tank near the bottom at one end and exited at the top through an outlet in the hatchway wall. Oxygenation equipment like that described for the laboratory experiments was used in each tank to supplement O_2, which was measured with the same type of meter used in laboratory experiments.

Experimental Procedures

The transport tanks were made ready before fishing began by establishing a flow of seawater and 200-300% supersaturation of oxygen. Each fish caught was lowered on the fishing line through a tank's hatch and allowed to escape the barbless hook. On each day, the entire complement of fish was taken from a frenzy-feeding school (Strasburg and Yuen 1960) within a period of about 10 min. A tank-lot ranged from 7 to 12 fish, averaging 1.83-2.22 kg; estimated mean weight of captive fish was the actual mean weight of 20 other fish caught from the same school. Such an estimate is quite accurate because the size of individual fish within a skipjack tuna school is remarkably uniform (Brock 1954).

Within 2 h of capture, oxygen-uptake rate ($\dot{V}_{O_2}$) was measured for each of the 11 tank-lots of fish. In each tank the flow of oxygen was stopped and the time was measured for O_2 to decline from the saturation level (6.9 mg O_2/l) to a second level between 6.2 and 5.6 mg O_2/l. For three tank-lots of fish, a second measurement of $\dot{V}_{O_2}$ was made after resaturation of the tank with oxygen. Because the flow of water through the tanks was maintained throughout the 3- to 15-min period of O_2 measurement, calculation of $\dot{V}_{O_2}$ accounted for O_2 both supplied to and removed from the tank in the flow of water:

$$\frac{d[O_2]_c}{dt} \cdot C = ([O_2]_I - [O_2]_c)\dot{Q} - N \cdot \overline{W} \cdot \dot{V}_{O_2}$$

which gives, upon integration and solution for $\dot{V}_{O_2}$,

$$\dot{V}_{O_2} = \frac{([O_2]_I - [O_2]_c) \cdot \dot{Q}}{N \cdot \overline{W} \cdot (1 - \exp(-\dot{Q} \cdot C^{-1} \cdot t))}$$

where $\dot{V}_{O_2}$ = oxygen-uptake rate (milligrams O_2/gram per hour),
$[O_2]_I$ = concentration of O_2 in incurrent water (milligrams O_2/liter),
$[O_2]_c$ = concentration of O_2 in tank and in excurrent water (milligrams O_2/liter),
$\dot{Q}$ = water exchange rate (liters/hour),
N = number of fish in tank,
$\overline{W}$ = estimated mean weight of fish (grams),
C = operating volume of tank (liters),
t = time (hours) for oxygen concentration in tank to decline from $[O_2]_I$ to $[O_2]_c$.

Low-Oxygen Tolerance Experiments

Apparatus

The tank used for the low-oxygen tolerance experiments was identical to the smaller respirometer tank but was uncovered and was supplied with unaerated water (0.5 mg O_2/l) directly from the seawater well. During the time it took to fill the tank, the water took up atmospheric oxygen and O_2 increased to 1.4 mg O_2/l.

Experimental Procedure

Twelve experiments were made, using 21 skipjack tuna (Table 2). The fish for six of the experiments were the same pair that had been used for a preceding series of oxygen-uptake experiments. For the other six experiments, skipjack tuna were taken directly from a holding tank. The fish were rested in the uncovered respiration tank at air-saturated O_2 levels (6.8-7.0 mg O_2/l) for about 2 h prior to being transferred to an immediately adjacent low-oxygen test tank. Because of a fish shortage, we were forced to use single rather than paired animals for the last three experiments.

TABLE 2.—Swimming speed and resistance time to low oxygen of skipjack tuna at various oxygen concentrations. Those fish which continued swimming for 240 min were considered to have survived. Length measure is fork length.

Experiment	Oxygen level (mg/l)	Weight of fish (g)	Resistance time (min)	Swimming speed range ($L \cdot s$)
1	3.0	1,496	74	1.8-2.0
		1,910	115	
2	2.0	2,467	10	1 8-3.7
		1,890	20	
3	2.5	3,057	57	1.8-2.7
		3,523	60	
4	1.4	1,537	9	2.8-5.0
		1,161	10	
5	3.0	1,545	55	1.5-2.8
		1,887	70	
6	3.5	3,430	65	1.5-2 0
		1,616	155	
7	3.5	890	91	1.1-2.0
		902	Survived	
8	3.5	812	53	1.2-2.5
		791	65	
9	4.0	830	Survived	1.0-1.5
		1,020	Survived	
10	3.0	2,132	106	1.5-2.6
11	2.0	1,765	7	2.0-4.0
12	2.5	1,353	28	1.7-2.2

The experiments were done with O_2 ranging from 1.4 to 4.0 mg O_2/l and temperatures between 23° and 24° C. When O_2 in the low-oxygen tank reached the required levels, the fish were netted from the resting tank into the test tank. Each transfer took <5 s, and two fish were transferred within 30 s.

The O_2 and the behavior and swimming speeds of the fish were observed continuously. During an experiment, the water took up atmospheric oxygen at a rate dependent on the air-water pressure gradient. However, at all of the experimental O_2 levels there would have been a decrease of O_2 concentration due to the fish's respiration had we not gradually introduced oxygen as it was depleted by the fish; by so doing we continuously maintained O_2 concentration within ± 0.2 mg/l of the nominal experimental level.

A fish's resistance time was the period from introduction into the low-oxygen tank until the animal lost equilibrium and settled to the bottom. A fish was considered to have survived if it was still swimming after 240 min, at which time the experiment was terminated. At the conclusion of each experiment, weight and fork length of each fish were measured.

RESULTS

Oxygen-Uptake Experiments in Laboratory

Condition Factor

It has been our experience that skipjack tuna do not do well in captivity for extended periods. Obviously valid behavioral and physiological data require that the experimental animals be in good health. As mentioned above, our fish were actively feeding and had been captive for less than a month. Some additional evidence relative to their general condition is provided by comparing the length-weight relationship of the experimental fish with the relationship obtained by Nakamura and Uchiyama (1966) for freshly caught skipjack tuna. For our captive fish, $\log W$ (grams) $= -2.657 + 3.532 / \log L$ (centimeters); for wild skipjack tuna, $\log W$ (grams) $= -2.317 + 3.368 / \log L$ (centimeters) ($\log = \log_{10}$). This comparison indicates that our experimental fish were, on average, about 14% lighter at a given length than wild fish of the same mean length (ca. 48 cm), the difference in weight-at-length decreased with increasing fork length. Part of the weight discrepancy resulted from the near emptiness of the guts of the experimental fish. Raju (1964) reported that pole-and-line caught skipjack tuna weighing about 1.4 kg had stomach contents comprising about 1.5% of body weight on the average and 6.3% of body weight at maximum.

General Behavior

The behavior of a group or pair of fish over the four experimental runs changed very little, and behavioral variation among the 10 series of experiments was slight.

The fish, usually in close company, continuously circled the respirometer 20-30 cm from the sides. Their course in the smaller respirometer was usually elongate but quite frequently shifted to a circle with a radius of 60-70 cm. Direction reversal and figure of eight patterns were not unusual. Rarely one fish would break away and swim separately, sometimes in a direction opposite the other fish, but such divergent patterns never persisted for long.

Swimming Speed

Swimming speed of skipjack tuna, averaged over all experiments, was 1.4 L/s. Speed was independent of O_2 over the experimental range (5.0-7.0 mg O_2/l), but stepwise multiple regression indicated significant ($P \leq 0.05$) effects of fish weight, length of time the fish had been in the respirometer, and the time-order of experimental series:

$$S = 3.55 - 0.53 / \log \overline{W} - 0.02t - 0.04 \cdot k$$

where S = swimming speed (lengths/second),
$\overline{W}$ = mean fish weight (grams),
t = time (hours) the fish had been in the respirometer,
k = time-order $(1, \ldots, 10)$ of the experimental series.

Thus, length-specific swimming speed decreased with increasing fish size and with increasing values of both time-related variables. Solution of the regression equation at mean values of t (9.28 h) and k (5.5) yielded $S = 3.14 - 0.53 / \log \overline{W}$ (Figure 2).

Respiration Rate

Mean respiration rate over all experiments was 0.52 mg O_2/g per h (Table 1). The data suggested

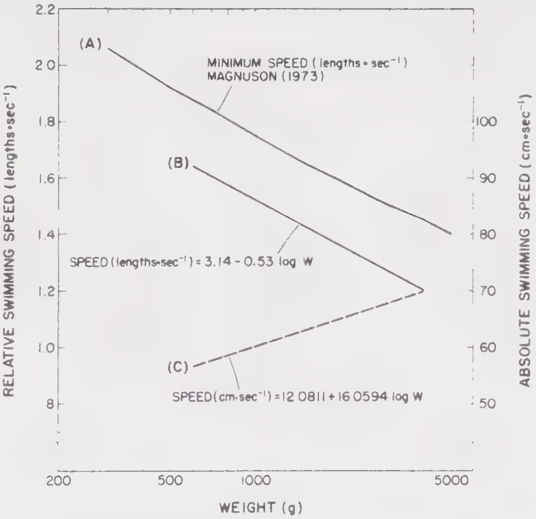

FIGURE 2.—Relation between voluntary swimming speed and body weight in skipjack tuna. Line A connects point-solutions from Magnuson's minimum speed function (Magnuson 1973). Line B is the relation between relative swimming speed and weight observed in the present study. Line C is the relation between absolute speed and weight observed in the present study. Length measure is fork length.

a slight but statistically nonsignificant decrease in respiration rate with decreasing oxygen concentration. Thus, our assumption of respiratory independence at oxygen concentrations down to 5.0 mg O_2/l seems valid; however, our experimental design did not permit proper analysis of the relation between respiration rate and O_2.

Of the other variables included in a stepwise regression analysis (fish weight, swimming speed, total time in respirometer, time of day, experimental order), only fish weight and swimming speed significantly ($P \leq 0.05$) affected respiration rate:

$$\log \dot{V}_{O_2} = -1.20 + 0.19 \log \overline{W} + 0.21 S$$

where $\dot{V}_{O_2}$ = oxygen-uptake rate (milligrams O_2/gram per hour),
$\overline{W}$ = mean fish weight (grams),
S = swimming speed (lengths/second).

We hasten to point out an irregularity in the relation just presented. While we offer the equation as a best available predictor of independent weight and speed effects on oxygen uptake in skipjack tuna, we recognize that $\overline{W}$ and S in our fish were not independent. As indicated in the last section, the fish tended to swim at a characteristic speed inversely proportional to the logarithm of body weight (Figure 2): $S = 3.14 - 0.53 / \log \overline{W}$. When this and the previous equation are combined to express the relation between oxygen-uptake rate and body weight for skipjack tuna swimming at their characteristic speeds, we are left with $\log \dot{V}_{O_2} = -0.54 + 0.08 / \log \overline{W}$. Thus, the speed-inclusive effect of $\overline{W}$ on oxygen-uptake rate actually observed in our experiments was quite small (Figure 3). A multiple regression analysis with speed deleted from the independent-variable list yielded no significant relation between $\dot{V}_{O_2}$ and $\overline{W}$ ($P > 0.05$). In contrast, the weight-inclusive effect of speed on $\dot{V}_{O_2}$ was readily apparent in a simple plot of $\log \dot{V}_{O_2}$ versus S (means) for all experiments (Figure 4).

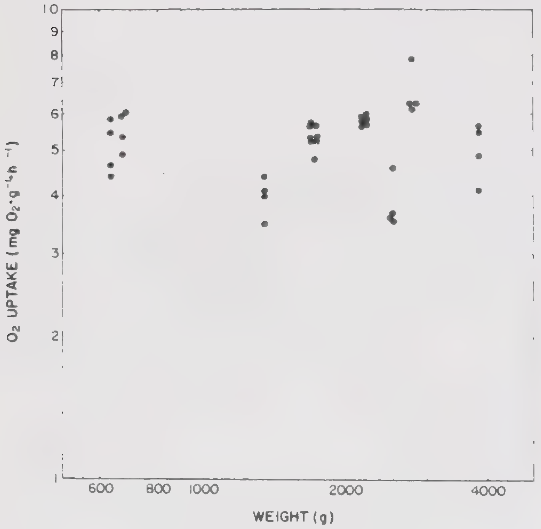

FIGURE 3.—Lack of significant relation between oxygen-uptake rate and weight of skipjack tuna swimming at voluntary speeds. Weights are means for the fish in each experimental series.

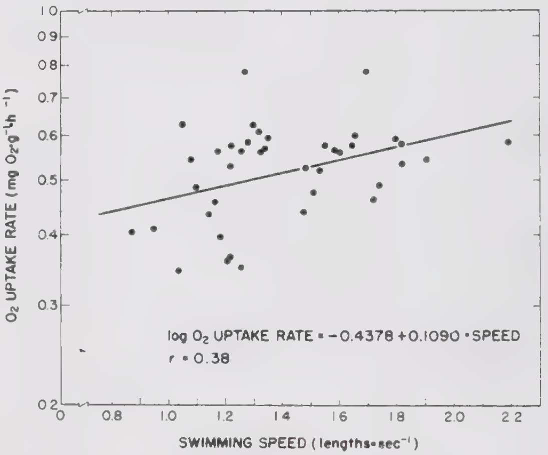

FIGURE 4.—Relation between oxygen-uptake rate and relative swimming speed of skipjack tuna (ranging from 60 to 4,000 g). Data are means for each experiment. Length measure is fork length.

Oxygen Consumption and Activity of Just-Caught Skipjack Tuna

Skipjack tuna, during their first 2.2 h of captivity, consumed oxygen at rates between 0.9 and 2.5 mg O_2/g per h, the median for the 14 determinations being 1.3 mg O_2/g per h at 75 min (Figure 5). Swimming speeds were correspondingly great—between 2 and 5 L/s.

Rate of oxygen consumption was not significantly correlated with time since capture (Kendall's $\hat{\tau} = -0.20$, $P \approx 0.18$; Siegel 1956) when all 14 rate determinations were considered as random observations from the same bivariate distribution. However, some features of the experiment suggested a decline in the rates of both oxygen con-

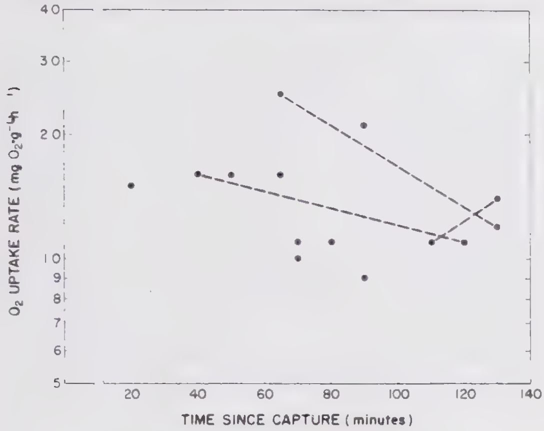

FIGURE 5.—Relation between the rate of oxygen uptake and the time elapsed after capture of skipjack tuna. Dashed lines connect paired determinations of oxygen-uptake rate for the same tank-lot of fish.

sumption and activity during the 2-h interval following capture. An initial period of frantic swimming, lasting 10-15 min, had already ended before we were able to collect our earliest respiration data. Still, the first five determinations of oxygen-consumption rate (within about 1 h of fish capture) were 1.5 mg O_2/g per h or more. In two cases, a tank-lot of fish respired at a much reduced rate during the second of two sampling intervals separated by about 1 h. (In a third set of such paired observations, oxygen uptake during the second was 0.3 mg O_2/g per h more than during the first, but these determinations were separated by only 20 min.) In conclusion, we believe the oxygen-uptake rate of our fish immediately after their capture was underestimated by the overall median value of 1.3 mg O_2/g per h and, in fact, may have exceeded 2.0 mg O_2/g per h.

Low-Oxygen Tolerance Experiments

General Behavior

Comparative behavioral responses of the fish in low-oxygen ($\leq$3.5 mg/l) water were quite consistent. However, the sequence of behavior was more accelerated and the fish's reactions were often more violent at the lower oxygen concentrations.

At the two lowest O_2's (1.4 and 2.0 mg/l) the fish showed symptoms of considerable stress within about 30 s of introduction. Stress was manifested as very fast swimming (2.6 *L*/s), wide mouth-gape, and little or no attempt to school. During the last few minutes before the skipjack tuna died, they assumed a steep angle of attack with their snouts out of the water and swam jerkily, with intermittent bursts of speed up to 6 *L*/s. Complete collapse came abruptly; the fish simply ceased swimming and settled to the bottom. At 2.5 and 3.0 mg O_2/l, the initial stress reactions were milder and the fish started schooling within a few minutes after introduction. Swimming speeds were still relatively high (1.7-2.8 *L*/s), and the sequence and types of behavior were similar to those at the lowest O_2. At 4.0 mg O_2/l, both skipjack tuna swam and otherwise behaved as if they were in oxygen-saturated water.

Resistance Time and Swimming Speed

There was a marked, direct relation between the logarithms of resistance time and oxygen concentration at oxygen levels up to 3.5 mg O_2/l (Table 2, Figure 6). At 3.5 mg O_2/l, four of the experimental fish had resistance times in the same range as the fish exposed to 3.0 mg O_2/l, but one fish survived for the 240-min duration of the experiment. The survivor showed few overt signs of stress but did swim faster than the fish in oxygen-saturated water. At 4.0 mg O_2/l, both experimental fish survived 240 min.

The 21 skipjack tuna used in the 12 experiments ranged in weight from 791 to 3,523 g (Table 2). There was no significant correlation between weight and resistance time to low-oxygen levels.

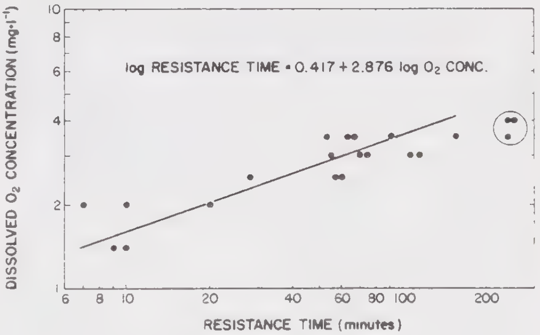

FIGURE 6.—Relation between resistance time to low-oxygen concentration and dissolved oxygen concentration. Resistance time was the period from the fish's introduction into the low-oxygen tank until it stopped swimming and settled to the bottom. Circled points indicate three fish that were still swimming after 240 min. The regression line was fitted to the points for fish that died.

Mean swimming speed increased as O_2 decreased (Figure 7), reaching 3.9 *L*/s at the lowest O_2, 1.4 mg O_2/l. Mean speed at 4.0 mg O_2/l was slightly less than at higher O_2 values (oxygen-uptake experiments); therefore, the critical O_2 for an increase in swimming speed appeared to lie between 4.0 and 3.5 mg O_2/l.

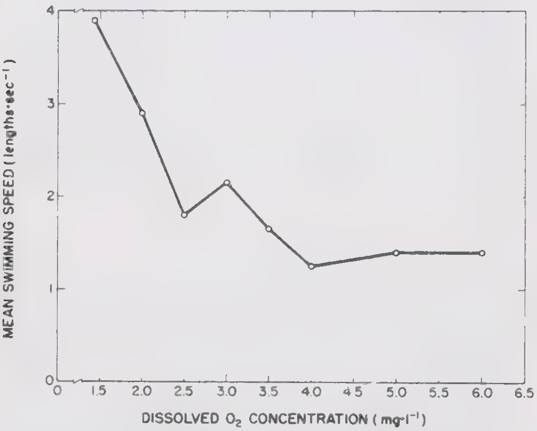

FIGURE 7.—Relation between mean swimming speed and dissolved oxygen concentration. The data for O_2 of 6.0 and 5.0 mg · l^{-1} are from the oxygen-uptake experiments. Those at lower concentrations are derived from the low-oxygen tolerance experiments. Length measure is fork length.

DISCUSSION

Terminology Relevant to Tuna Metabolism

In this paper we have strived to quantify the activity and respiration levels of our fish. The question of terminology remains. Doudoroff and Shumway (1970) have emphasized that "different meanings have been attached by different authors to the same term or different terms have been used in the same sense. . . ." The question of terminology is further complicated in tunas because they, unlike typical fishes, must maintain some minimum forward motion for hydrodynamic lift (Magnuson 1973) and for gill perfusion (Brown and Muir 1970; Stevens 1972); a stationary tuna both sinks and suffocates. Thus, the notion of "resting" metabolic rate (Doudoroff and Shumway 1970) is not applicable to tunas.

What we have collected in our laboratory experiments were data on "routine" (Fry 1957, 1971) activity and metabolism. Fry (1971) defined routine metabolic rate as "the mean rate observed in fish whose metabolic rate is influenced by random activity under experimental conditions in which movements are presumably somewhat restricted and the fish protected from outside stimuli." Our fish were in a postabsorptive state (except for bits of food they may have eaten during the transfer process) and were as quiescent as tunas are ever likely to be when confined in a small tank. Perhaps, our laboratory data reflect minimum metabolism for skipjack tuna in that the fish were swimming at speeds actually below the hydrodynamic minima calculated by Magnuson (1973) for skipjack tuna (Figure 2). On first consideration, it would seem unlikely that tunas—which lack ventilatory pumps and are, therefore, obligate ram-ventilators (Brown and Muir 1970)—could achieve minimum swimming speed without also achieving minimum rate of oxygen uptake. However, Stevens (1972) has shown that skipjack tuna have the capability for doubling the amount of oxygen they extract per unit flow of water irrigating the gills (utilization efficiency, 0.4-0.8) with only a 17% reduction in ventilation rate (from 3.0 to 2.5 l H_2O/kg per min). Thus, it is conceivable that a skipjack tuna could decrease swimming speed and simultaneously increase oxygen uptake. We must, therefore, recognize the possibility that "excitement" (Fry 1971) associated with the alien and confining environment of our respirometers resulted in heightened rates of oxygen uptake compared with those that might obtain in wild, unexcited skipjack tuna swimming in the sea at the same speeds. However, the data we collected do not permit an objective evaluation of this possibility. For purposes of further discussion, we assume that our laboratory measurements of oxygen-uptake rate contained no component of "excitement" metabolism independent of swimming speed. Lack of change in respiration rate among sequential experiments indicates that any activity-independent excitement component of metabolism that may have been present was habituation-time invariate. This has encouraged us to go so far in the following section as to estimate the hypothetical "standard" (= "basal"—see Fry 1971; Brett 1972) metabolism of skipjack tuna from our respiration data; this we did, as Fry (1971) recommends, by simply extrapolating to zero speed the regression equation relating respiration rate and swimming speed.

Rates of oxygen uptake measured in the "just-caught" fish can scarcely be considered "routine" but still may have underestimated the skipjack tuna's maximum or "active" (Fry 1971; Brett 1972) rate of oxygen consumption. Wild skipjack tuna similar in size to our experimental fish can swim at sustained speeds probably exceeding 10 L/s (Yuen 1970); our just-caught fish swam at speeds ≤ 5 L/s during the intervals when oxygen-uptake rates were measured. However, the experimental fish may have been repaying an oxygen debt incurred during the feeding frenzy preceding capture or during the early minutes of captivity; recovery from oxygen debt could have heightened oxygen-uptake rates to levels above those commensurate with sustained swimming at the observed speeds (Brett 1972).

"Standard" Metabolism

Even though tunas never lie stationary in the water, it is of interest from the bioenergetic and comparative standpoints to separate the routine metabolic rate into standard and activity-related components. From the equation on p. 38, with swimming speed set equal to 0.0,

$$\log \dot{V}_{O_2} = -1.20 + 0.19 \log \overline{W},$$

where $\dot{V}_{O_2}$ = oxygen-uptake rate (milligrams O_2/gram per hour),
$\overline{W}$ = mean fish weight (grams).

Solutions of this equation at our experimental extremes for $\overline{W}$ are $\dot{V}_{O_2} = 0.21$ mg O_2/g per h at $\overline{W} = 632$ g and $\dot{V}_{O_2} = 0.30$ mg O_2/g per h at $\overline{W} = 3{,}834$ g. These values are extraordinary for two reasons: 1) They are at the extreme upper limit for nontuna (cf. fig. 4 of Brett 1972), a fact that becomes even more remarkable when one considers that other teleost values are almost all for small (10-100 g) individuals, and 2) the weight exponent is a positive 0.19, not a negative value in the neighborhood of -0.2 characteristic of typical fishes (Fry 1957, 1971; Winberg 1960). While weight exponents for active metabolic rate in salmonids may frequently approach 0.0 (Job 1955; Brett 1965; Rao 1968), we know of no data to suggest weight exponents as large as $+0.2$ for metabolic rate in nonscombrid fishes. The validity of a large, positive value for the weight exponent of "standard" metabolic rate in skipjack tuna is supported by independent data, via direct calorimetry, on heat production rates; the red muscle of sedated skipjack tuna (maintained by gill perfusion) metabolized at a rate proportional to $W^{0.13}$ (Neill et al. 1976).

In marked contrast with our estimate of skipjack tuna's weight exponent for standard metabolism is that reported by Brill (1979)—negative 0.44, a value at the other extreme for fishes. Considering that Brill's and our groups of fish were similar in size range and preexperimental history, we must deduce that the large discrepancy between estimates relates principally to the difference in experimental methodologies: Brill took, as the standard metabolic rate, the stabilized minimum $\dot{V}_{O_2}$ of perfused skipjack tuna that had been first injected with the neuromuscular blocking agent gallamine triethiodide, then spinalectomized.

Activity-Related Metabolism

Our respiration experiments estimated only rates of oxygen uptake, not rates of instantaneous metabolic demand for oxygen. Neill et al. (1976) estimated that the oxygen demand of red muscle in highly active (chased) skipjack tuna can reach 7 mg O_2/g per h for periods on the order of 1-2 min. For even shorter periods, involving only true burst swimming, the rate of oxygen demand must be even higher. Brett (1972) has estimated that burst-swimming fishes' instantaneous rate of oxygen demand (on a whole-body basis) exceeds the maximum rate of supply by a factor of 10. Any excess of demand over supply accumulates as an oxygen debt that ultimately must be repaid.

Our observations on just-caught fish provided (probably conservative) estimates of the maximum rate at which skipjack tuna can supply oxygen to meet their metabolic demands. Like the skipjack tuna's "standard" metabolic rate, its maximum (active) rate of oxygen uptake must be substantially beyond that typical of fishes. Just-caught skipjack tuna respired at a median rate of 1.3 mg O_2/g per h; the highest five values (those obtained during the fish's first hour of captivity) were between 1.5 and 2.5 mg O_2/g per h. Brett (1972), in reviewing his own and others' work, reported that fishes' maximum rates of oxygen consumption reach a "probable ceiling" near 1.0 ± 0.2 mg O_2/g per h.

The activity-respiration relationship obtained at sea for just-caught skipjack tuna was reasonably consistent with that extrapolated from the laboratory experiments (Figure 8). However, data of the two kinds may have agreed less well had

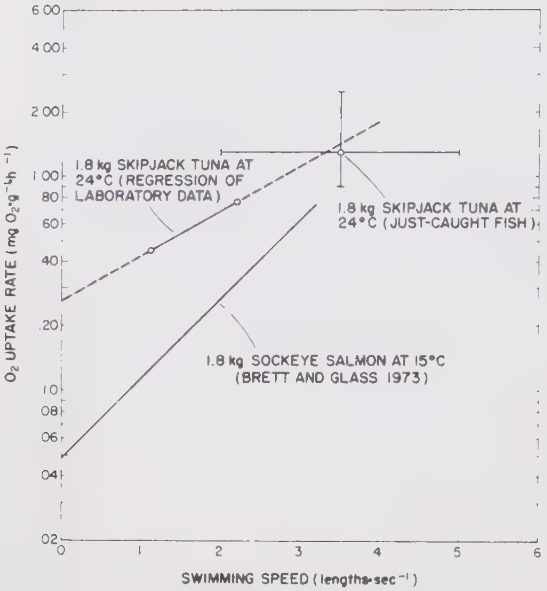

FIGURE 8.—Comparison between respiration-speed relations for 1.8 kg skipjack tuna calculated from the present study and for 1.8 kg sockeye salmon computed from equations given by Brett and Glass (1973). Ranges of observed values are indicated by the lines extending from the median value for just-caught skipjack tuna. Length measures are fork length.

we been able to accurately measure swimming speeds in just-caught fish. The basis for our cautious appraisal of such apparently good "fit" is suspicion that the linear model, $\log \dot{V}_{O_2} = a + b \cdot \text{speed}$, which seems adequate for many fishes (Brett 1972; Brett and Glass 1973; Webb 1975), cannot hold for skipjack tuna over the entire range of swimming speeds that they can sustain. Personal observations on these fish and Yuen's (1970) report of a school of skipjack tuna (ca. 44 cm fish) that traveled 28 km in 107 min (average minimum speed = 4.4 m/s) convince us that 40-50 cm skipjack tuna can swim for at least an hour at speeds near 10 *L*/s. If that is so, our linear model predicts oxygen uptake in 1.8 kg skipjack tuna (median size of just-caught fish) at a maximum sustained rate of at least 33.0 mg O_2/g per h. Active metabolic rate of skipjack tuna may substantially exceed Brett's (1972) predicted maximum for fishes, but we are confident it does not do so by a factor of nearly 30. The most logical interpretation of this conundrum is nonlinearity in the relation between $\log \dot{V}_{O_2}$ and speed; as skipjack tuna swim faster, they must become more efficient in their use of oxygen and energy. The same is probably true for other fast-swimming fishes, such as Peterson's (1976) striped mullet, *Mugil cephalus*. Even in the relatively sluggish goldfish, *Carassius auratus*, oxygen-uptake rate actually declines as the fish pass from spontaneous activity at low apparent speeds to induced swimming (against currents) at higher speeds (Smit 1965).

There is, of course, an alternative explanation: Our laboratory experiments overestimated the true coefficient for speed. In fact, taking the lower 95% confidence limit on the speed coefficient—0.11—yields a comparatively modest 3.31 mg O_2/g per h for predicted $\dot{V}_{O_2}$ at 10 *L*/s. But a true speed coefficient as low as 0.11 is not only inconsistent with the comparable coefficient in other fishes (Fry 1971; Brett 1972) but also with other, independent data (Chang et al.[4]) on metabolism-speed relations in skipjack tuna. The speed coefficient estimated from that study was 0.22, a value remarkably similar to our mean estimate.

To close our consideration of activity-related metabolism in skipjack tuna, we offer a comparison between respiration-speed relations of a 1.8 kg skipjack tuna at 24° C and a 1.8 kg sockeye salmon, *Oncorhynchus nerka*, at 15° C (Figure 8). We chose the sockeye salmon because its active metabolic rate "is one of the highest [for fishes] on record, exceeding that determined for other salmonids by 30% to 40%" (Brett and Glass 1973). The sockeye salmon respiration-speed relation was computed from equations given by Brett and Glass (1973); 15° C-values were used because this is near the sockeye salmon's thermal optimum for fast swimming and several other vital functions (Brett 1971). Skipjack tuna seem to swim and metabolize at rates nearly independent of temperature (Dizon et al. 1977; Chang et al. footnote 4).

At all speeds common to the two fishes, skipjack tuna have the higher metabolic rate—3.7 times higher at 1.1 *L*/s (the skipjack tuna's minimum speed) decreasing to 1.7 times higher at 3.2 *L*/s (the sockeye salmon's maximum sustained speed). If the basis of comparison is the energy cost of swimming (oxygen-uptake rate associated with any particular speed minus standard uptake), the difference between these fishes is lessened but the qualitative relation is unchanged: at

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[4] Chang, R. K. C., B. M. Ito, and W. H. Neill. Manuscr. in prep. Temperature independence of metabolism and activity in skipjack tuna, *Katsuwonus pelamis*. Southwest Fish. Cent., Natl. Mar. Fish. Serv., Honolulu, HI 96812.

1.1 and 3.2 L/s, the cost for skipjack tuna are, respectively, 2.5 and 1.4 times those for sockeye salmon. We can only conclude that 1.8 kg skipjack tuna swim at intermediate speeds less efficiently than 1.8 kg sockeye salmon—this despite the fact that, among fishes, the skipjack tuna represents the apex of evolutionary engineering for speed (Magnuson 1973; Stevens and Neill 1978). Presumably, the evolution of skipjack tuna (like that of fast cars) has involved sacrifice of energetic efficiency at low speeds in favor of increased efficiency at high speeds, permitting a dramatic increase in maximum attainable speed.

Interrelation of Metabolic Rate, Swimming Speed, and Body Weight

Voluntary speeds (S, lengths/second) of skipjack tuna swimming in our laboratory respirometers were inversely related to fish weight by the relation $S = 3.14 - 0.53/\log\overline{W}$. Magnuson (1973), working from basic hydrodynamic relations, predicted minimum speed for steady-state swimming in various tunas; his model for skipjack tuna yielded a speed versus fish-weight relation very similar in slope to that we observed (Figure 2). The difference in means may be attributable to differences in condition factor and/or body-water content (Kitchell et al. 1977) between our captive fish and the wild skipjack tuna on which Magnuson's calculations were based.

Oxygen-uptake rates ($\dot{V}O_2$, milligrams O_2/grams per hour) of our laboratory fish were influenced not only by swimming speed but also by fish weight independent of speed: $\log \dot{V}O_2 = -1.20 + 0.19 \log W + 0.21S$. We have concluded above that 1) the intercept value ("standard" rate at any weight) is unusually large for fishes; 2) the weight coefficient is opposite in sign from that typical of fishes (and of organisms, generally); and 3) the interdependency of $\log \dot{V}O_2$ and S on weight is compensatory, resulting in no statistically demonstrable difference among oxygen-uptake rates for skipjack tuna of various weights (600-4,000 g) swimming at their characteristic speeds.

Conclusion (3) led us to explore the relation between oxygen-uptake rate per unit distance ($\dot{V}\acute{O}_2$, milligrams O_2/gram per kilometer) and swimming speed for skipjack tuna of different sizes. Exponentiating the linear regression equation relating $\dot{V}O_2$ in milligrams O_2/gram per hour to W and S, $\dot{V}O_2 = 0.063 \cdot W^{0.19} \cdot 10^{0.21S} = 0.063 \cdot W^{0.19} \cdot e^{0.48S}$. Multiplying the last equation by $27.78 \cdot \mathrm{km}^{-1} \cdot S^{-1} \cdot L^{-1}$ generated an equivalent expression for $\dot{V}\acute{O}_2$ in milligrams O_2/gram per kilometer:

$$\dot{V}\acute{O}_2 = 1.75 \cdot L^{-1} \cdot S^{-1} \cdot W^{0.19} \cdot e^{0.48S}.$$

Finally, we used the exponentiated length-weight relationship for experimental fish: $\log W = -2.657 + 3.532 \log L$; thus, $W = 0.0022L^{3.532}$ to eliminate W:

$$\dot{V}\acute{O}_2 = 0.55 \cdot L^{-0.33} \cdot S^{-1} \cdot e^{0.48S}.$$

Solutions of this equation for $\dot{V}\acute{O}_2$ at various values of L and S are shown graphically in Figure 9. Small fish are less efficient (higher $\dot{V}\acute{O}_2$) at any particular speed than are larger fish, but fish of all sizes reach their particular minimum $\dot{V}\acute{O}_2$ at the same relative speed—about 2.1 L/s. The relation between this, the optimum speed (S_{opt}) for covering distance, and the value of the coefficient, 0.48, for the exponential term in S is simple—each is the reciprocal of the other:

$$\frac{d\dot{V}O_2}{ds} = 0.55 \cdot L^{-0.33} \text{ per } \frac{0.48S \cdot e^{0.48S} - e^{0.48S}}{S^2};$$

$$\text{at } \frac{d\dot{V}\acute{O}_2}{ds} = 0,\ 0.48S \cdot e^{0.48S} = e^{0.48S};$$

$$\text{therefore, } S_{\mathrm{opt}} = \frac{1}{0.48} \approx 2.08.$$

For skipjack tuna between 30 and 60 cm length, the characteristic speeds and $S_{\mathrm{opt}} = 2.08$ correspond with $\dot{V}\acute{O}_2$ rates that are maximally (for 60 cm fish) different by only 13% of min $\dot{V}\acute{O}_2$ (Figure 9). The question arises as to whether the observed characteristic speeds, rather than "S_{opt}," might be the (evolutionary) "design" speeds that minimize $\dot{V}\acute{O}_2$. The characteristic speeds agree remarkably well (better than does "S_{opt}") with the optimum speed predicted by Weihs' (1973b) model; Weihs, reasoning from thrust and drag relations for fishes, argued that speed is optimized (energy expended per unit distance is minimized) when "the rate of energy expenditure required for propulsion [and associated physiological work?] is equal to the standard (resting) metabolic rate." For our skipjack tuna, S at $\dot{V}O_2$ equivalent to twice the hypothetical standard rate was 1.43 L/s, a value that falls midway in the range of speeds

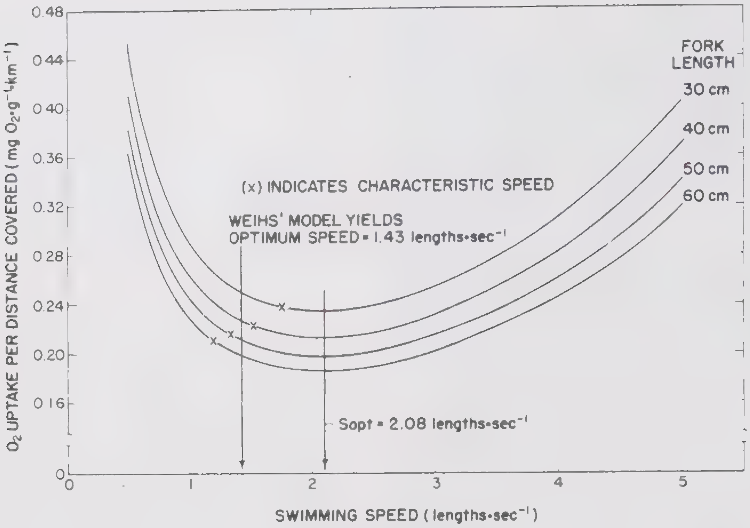

FIGURE 9.—Relation of rate of oxygen uptake per unit distance ($\dot{V}O_2$) swam to swimming speed for skipjack tuna of various lengths. The x's indicate characteristic swimming speeds of fish in the present study. S_{opt} is the optimum speed for covering distance in terms of minimum $\dot{V}O_2$. The arrow at 1.43 lengths · $\sec^{-1}$ is the optimum speed predicted by Weihs' (1973b) model.

characteristic of fish between 30 and 60 cm length (Figure 10).

In a subsequent paper, Weihs (1977) showed that fishes' optimum swimming speeds on an absolute basis ought to be proportional to $L^{0.43}$. The characteristic speeds of our tuna, when computed in centimeters per second and treated as a power-function of fish length, are proportional to

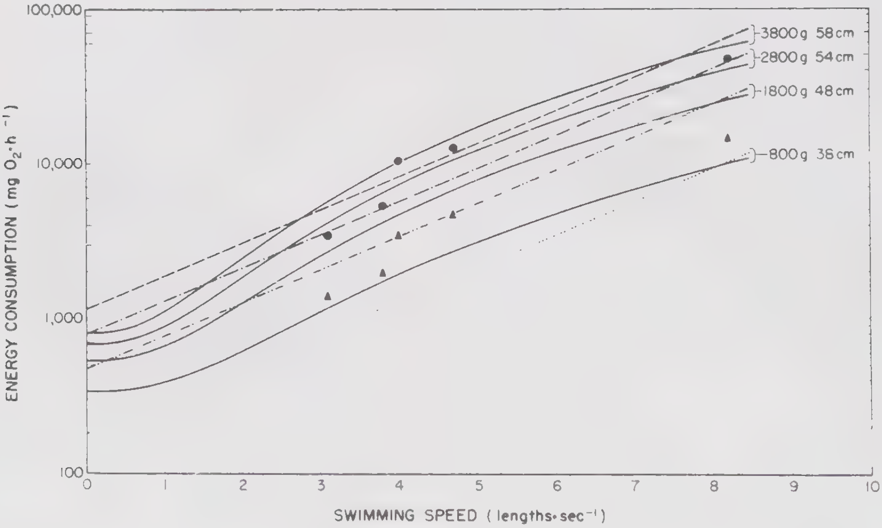

FIGURE 10.—Comparison between the measured oxygen uptake relationship extrapolated between 0 and 8.5 lengths · $\sec^{-1}$ (broken lines) and the theoretically expected power consumption (solid lines) for four skipjack tuna. Triangles (▲) are the theoretical power consumption based on a detailed analysis of drag forces for a 40 cm, 1,003 g skipjack tuna (Magnuson 1978). Points (●) are based upon a detailed analysis of thrust forces (Magnuson 1978). Length measures are fork length.

$L^{0.45}$ and, thus, fit Weihs' model almost perfectly.

We conclude by noting that our discussion of optimum swimming speeds for covering distance relates only to skipjack tuna swimming at constant depth (as those in our respirometers were required to do). Weihs (1973a) has calculated that negatively buoyant fishes like the skipjack tuna could achieve an energy savings of 20% (compared with swimming at constant depth) by alternately gliding downward at an angle of about 11° (to the horizontal), then actively swimming upward at an angle near 37°.

Resistance to Low Oxygen

In areas of the world ocean with surface waters not stressfully warm for skipjack tuna there is always available air-saturated water that overlies oxygen-depleted strata (Barkley et al. 1978). Therefore, the 4-h exposure period we adopted in this study would seem to include all intervals of low-oxygen exposure that skipjack tuna ever need endure at sea.

The data suggest for skipjack tuna a threshold of response to hypoxic stress at about 4.0 mg O_2/l (Figure 7); this value is at or below that representative of fishes (Davis 1975). In our experiments, the skipjack tuna's response to low oxygen was an increase in swimming speed; this would seem adaptive in that increased swimming speed initiated by hypoxic stress would facilitate return of fish from deep, oxygen-depleted water to air-saturated surface water.

The 4-h median tolerance limit to low oxygen was also near 4.0 mg O_2/l (Figure 6). This value, in keeping with the skipjack tuna's exceptionally high metabolic rate, is apparently higher than that of any other fish yet investigated (Doudoroff and Shumway 1970).

Angular Acceleration and Excess Body Temperature

Compared with other studies of fish metabolism, our experiments with skipjack tuna involved two unusual elements: 1) The fish were forced, by the relatively small size of the tanks, to swim a curved path, and 2) they probably had core temperatures up to several degrees higher than the temperature of the surrounding water.

Weihs (1981) has suggested that our continuously turning fish expended more propulsive energy than they would in swimming a straight path at the same speed. A turning tuna must counter centrifugal forces by "banking" with its pectoral fins to produce a component of lift directed inwards along the turning radius. Therefore, our results may overestimate the oxygen-uptake rates and perhaps also the lower lethal oxygen concentration for skipjack tuna at sea. However, we doubt that the magnitude of the overestimate can be very great, for fish in the large and small respirometers (with radii of typical swimming paths about 2 and 0.8 m) respired at similar rates (Table 1). Furthermore, metabolic rates of fish in our experiments were consistent with those inferred from weight and energy "loss" rates of starved skipjack tuna living in tanks 7.3 m in diameter (Kitchell et al. 1978).

Oxygen-uptake rates of our test fish also compare well with theoretical estimates of the amount of energy consumed by similarly sized fish swimming a straight course at the same speeds (Figure 10). The observed oxygen-uptake relationship (milligrams O_2/hour) was extrapolated from 0 to 8.5 *L*/s for four skipjack tuna ranging in weight from 800 to 3,800 g (dashed lines). (Recall that mean speeds of our fish were between only 0.9 and 2.2 *L*/s.) Superimposed on the empirical relationship are theoretical projections of energy consumption based on estimates of drag force. Theoretical energy uptake—in keeping with the reasoning of Webb (1975), Sharp and Francis (1976), Sharp and Vlymen (1978), and Dizon and Brill (1979)—was computed according to the following rationale:

1. Total power required is the sum of the power required for nonswimming processes (P_2) plus power required for thrust (P_1), the latter divided by an estimate of total aerobic efficiency $\equiv 0.2$ (Webb 1975).
2. Power required for nonswimming metabolic processes (the standard metabolic rate of a fasted fish from Brill (1979)),

$$P_2 = 1.53 \quad W^{0.563}$$

where P_2 = power (watts),
W = weight (kilograms).

Brill's (1979) relation is used despite some doubts about the validity of the exponent because it provides for skipjack tuna the only estimate of P_2 independent of our data.

3. Thrust power must be equal to drag force multiplied by velocity

$$P_1 = 0.5 \cdot \rho \cdot S \cdot U^3 \cdot C_d \cdot 10^{-7}$$

where P_1 = power (watts),
ρ = water density (1.0234),
S = surface area ($0.4\ L^2$) where L = length (centimeters),
U = velocity (centimeters/second),
C_d = drag coefficient.

4. The drag coefficient is estimated using Webb's (1975) formula, as

$$C_d = 10 \cdot \left(\frac{\rho L U}{\mu}\right)^{-0.5}$$

where μ = water viscosity (0.0096).

5. Assuming an oxycaloric equivalent of 3.4 cal/mg O_2, power in watts can be converted into oxygen uptake in milligrams O_2/hour by multiplying watts by 253.

The simple model of energy consumption presented here makes no pretention of precision because no attempt was made to accurately determine either the coefficient of drag or the surface area of the fish. Magnuson and Weininger (1978) and Magnuson (1978) did do that. We have included their estimates for power consumption of a 40 cm, 1,003 g skipjack tuna in Figure 10. The five triangles are estimates of power consumption based on Magnuson's (1978) determination of drag forces, the points based upon Lighthill's (1969) model of thrust forces (data from Magnuson 1978: table XI). Whether a sophisticated estimate of power consumption or a simple one is employed, the correspondence between the theoretically expected and the empirically derived power consumption is good. We take this as additional evidence that our experimental values are reasonable estimates of oxygen uptake of skipjack tuna swimming straight courses at sea.

Skipjack and other tunas are warm bodied, owing to their high metabolic rates coupled with large thermal inertia (Neill et al. 1976; Stevens and Neill 1978). Thus, our fish undoubtedly were warmer than the water in which they swam. Skipjack tuna used in the laboratory experiments probably had core-temperature excesses on the order of 2°-4° C (cf. Stevens and Fry 1971; Neill et al. 1976); the just-caught fish, being more active, may have had core temperatures as much as 10° C above ambient water temperature (cf. Stevens and Fry 1971). Interpretation of our results has not been complicated by consideration of the difference between tissue and environmental temperatures, because metabolism of skipjack tuna has been shown to be virtually independent of temperature (Gordon 1968; Chang et al. footnote 4).

CONCLUSION

Our findings emphasize the unique evolutionary position of the skipjack tuna (and, by extension, other tunas) among fishes. The skipjack tuna epitomizes what Stevens and Neill (1978) have termed "energy speculators": forms that "operate to maximize energy gain by gambling large energy expenditures...on the expectation of proportionately large energy returns." The skipjack tuna's "standard" metabolic rate is two to five times that of typical fishes of similar size. Moreover, the skipjack tuna is relatively inefficient in its use of oxygen and food-energy for swimming (at least at low speeds) and it dies at O_2 levels still well above those lethal to other fishes. Clearly, the skipjack tuna's ability to sustain high levels of activity has not been achieved without substantial physiological cost.

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EDDIES AND SPECIATION IN THE CALIFORNIA CURRENT

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ABSTRACT

Northern anchovy, Pacific sardine, and Pacific hake have population discontinuities in the vicinity of Punta Eugenia, Baja California. The same latitude has been described as a provincial boundary for several taxa, including coastal fishes, brachyurans, bryozoans, and molluscs. The distribution of wind stress over the surface waters of the California Current region has a persistent feature in the same area: the coastal impingement of a zone of surface water convergence, which elsewhere is parallel to the coast of the Californias and several hundred kilometers offshore. Semipermanent cyclonic eddies are evident north and south of Punta Eugenia, and it has been suggested that they play a role in the recruitment of pelagic larvae to the adult populations in these areas.

Limited communication between the eddies suggests a speciation mechanism that would be most effective on populations that time their spawning to coincide with strong eddy formation. One may also expect geminate species north and south of Punta Eugenia and few short-range endemics with long dispersal strategies along the coast of northern Baja California between the eddies.

RESUMEN

Existen discontinuidades en las poblaciones de anchoveta del norte, sardina y merluza en la zona de Punta Eugenia, Baja California. Esta latitud ha sido descrita como una frontera provincial de varios grupos taxonómicos, incluyendo peces costeros, braquiuros, briozoarios y moluscos. La distribución de esfuerzo del viento por las aguas de superficie de la región de la Corriente de California tiene una característica persistente en esta misma área, que es el encuentro con la costa de una zona de convergencia de aguas de superficie, que en otras partes ocurre paralela a la costa y a unos cientos de kilómetros afuera. Remolinos ciclónicos semipermanentes son evidentes al norte y al sur de Punta Eugenia, y se ha sugerido que éstos juegan un papel en el reclutamiento de larvas pelágicas a las poblaciones adultas en estas zonas.

La comunicación limitada entre los remolinos sugiere un mecanismo de especiación que sería más efectivo para poblaciones que fijan su época de desove durante los períodos en que se forman fuertes remolinos. Puede esperarse encontrar especies geminados al norte y al sur de Punta Eugenia y algunas especies endémicas de rango corto con estrategias de larga dispersión en la costa del norte de Baja California, entre los remolinos.

INTRODUCTION

Several coastal pelagic fish species display a population break in the vicinity of Punta Eugenia, Baja California. Distinct discontinuities in morphometric measurements, meristic counts, and proportion of selected protein polymorphs suggested restricted gene flow between populations north and south of approximately 28° N for *Engraulis mordax,* the northern anchovy (Hubbs 1925; McHugh 1951; Vrooman et al. in press), for *Sardinops caerulea,* the Pacific sardine (Clark 1947; McHugh 1950; Marr 1957, 1960; Sprague and Vrooman 1962; Vrooman 1964), and for *Merluccius productus,* the Pacific hake (Vrooman and Paloma 1977). Vrooman and Paloma (1977) referred to the southern population of *M. productus* as "dwarf hake" and suggested that it differs from *M. productus* and the more southern *M. angustimanus* at the species level. The southern populations of all three fishes *(Engraulis mordax, Sardinops caerulea,* and *Merluccius productus)* show similarities in some of the ways they differ from the northern population: growth is reduced after the first year resulting in a reduced maximum adult size, maturity occurs at an earlier age, and the life span is shorter; the southern forms have proportionally longer heads, longer snouts, and larger eyes.

The latitude of Punta Eugenia has been described as a provincial boundary for a wide variety of taxa including coastal fishes (Hubbs 1960), brachyurans (Garth 1960), bryozoans (Soule 1960), and molluscs (Hall 1964; Valentine 1966). These authors refer to a variously named warm-temperature fauna between Point Conception and Punta Eugenia and a distinct fauna of uncertain origin from Punta Eugenia south to Cabo San Lucas. Hubbs (1960) tentatively placed this region in the Panamic province but noted the "reduced tropical fauna," high endemism, and "insular characteristics" of the biota.

Superimposed on the distributions of coastal animals are the distributions of invertebrate species as-

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sociated with oceanic water masses. The distribution of oceanic euphausiids and copepods, indicators of subarctic, equatorial, and central waters, have a common terminus at Punta Eugenia (Brinton 1962, 1967, 1973; Fleminger 1964, 1967). The junction of these distributions appears to move northward or southward in concert with temperature anomalies as described in CalCOFI Atlas Number 1 (Anonymous 1963) and by Wyllie and Lynn (1971), although shallow-water forms show a much clearer response than do deeper forms (Brinton 1960).

HYDROGRAPHY

The general hydrography off the coast of the Californias is determined by the California Current and is related to the anticyclonic circulation of the central North Pacific; however, significant features can be associated with local wind patterns and topography (Sverdrup et al. 1942; Smith 1968). Long-term monthly mean distributions of wind stress show alongshore flow throughout the year, weakest in the winter and strongest in the summer (Nelson 1977). Resolved on a 1° grid, however, net Ekman transport, proportional to and at right angles to the wind stress, shows considerable spatial variability. In general, an area of divergence parallels the coast, bounded by a zone of convergence 200-300 km from the coastline. The position of change from offshore divergence of surface water to convergence corresponds with the position of maximum wind stress, which intensifies, winter to summer, as the gradient between the semipermanent high pressure cell over the eastern Pacific Ocean and the low pressure cell over the southwest United States increases. The zone of convergence impinges the coasts at Punta Eugenia; this feature persists throughout the year and may preclude any poleward movement of water near the coast (Nelson 1977).

Surface current patterns, which describe cyclonic eddies in the Los Angeles Bight and southwest of Punta Eugenia, confirm Nelson's prediction (Bakun and Nelson 1977). Surface flow of the California Current appears to be diverted offshore at Point Conception and again at Punta Eugenia, while semipermanent eddies are apparent south of these headlands (Reid et al. 1958). Owen's (1980) description of baroclinic eddies and their persistence is in accord with this description.

DISCUSSION

The above-mentioned taxa have planktonic larval stages. The coastal eddies may play a role in recruitment to coastal adult populations by entraining a fraction of the larvae, thus offsetting to some extent dispersion to the southwest via the California Current. Johnson (1960) has suggested such a mechanism for maintaining populations of *Panulirus interruptus*, the spiny lobster, in the Southern California Bight and southwest of Punta Eugenia. Boehlert (1977) recognized the possible importance of the Southern California Eddy to the recruitment of *Sebastes* spp., rockfishes. Early ichthyoplankton studies off the coast of the Californias found relatively few sardine eggs and larvae off northern Baja California and characterized these waters as a "marine desert" bounded by "rich" waters to the north and south (Anonymous 1952).

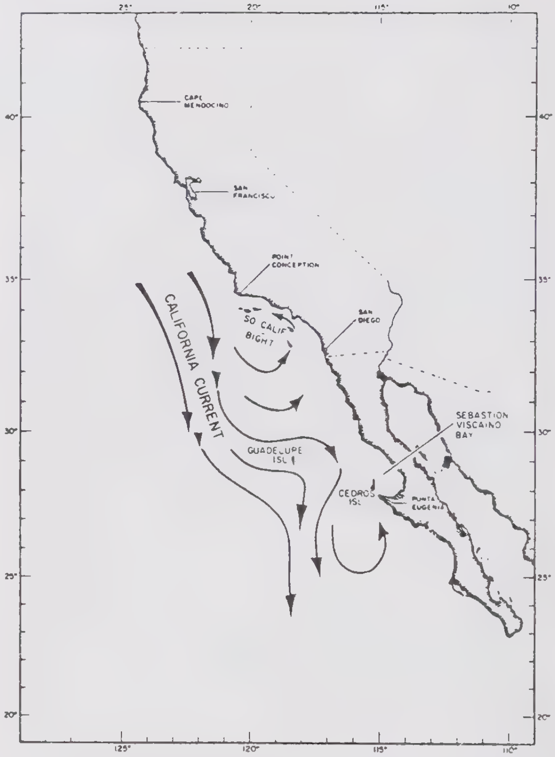

Figure 1. Large, persistent coastal eddies, south of Point Conception and Punta Eugenia, may entrain pelagic larvae and thus contribute to the recruitment to resident adult populations. Isolation of the eddies may constitute a speciation mechanism.

If the eddies are important to the process of recruitment, then the limited communication between them suggests a restricted gene flow between populations in the Southern California Bight and those south of Punta Eugenia. This postulated mechanism for speciation lends itself to several predictions:

1. Genetic differentiation between populations, within a species, should be greatest for those forms that time their spawning to coincide with

strong eddy formation as opposed to those forms that may time their spawning in response to other cycles (e.g. primary productivity).

2. There should be evidence of geminate species north and south of Punta Eugenia; e.g. *Labidocera trispinosa* and *L. johnsoni* (Fleminger 1975).
3. On the coast of northern Baja California, between the eddies, there should be a low proportion of dispersal types among sessile populations. A pelagic larval phase would imply dependence on long-range dispersal from the north; instead there should be selection for short pelagic phases or none at all.
4. The latitude of the hydrographic barrier may vary and be obscured by the convergence of oceanic water masses in the same general area which appears to be most pronounced in the upper layers.

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THE VALUE OF PATTERN IN THE DISTRIBUTION OF YOUNG FISH

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A hypothesis is proposed that the "patchy" character of pelagic larval fish distributions is adaptive and may be considered a life history trait co-evolved with a suite of other behavioral traits and physiological characteristics which together assure optimum larval survival. Specific differences in larval "patchiness" are implied and these differences may be explained in biological terms. A method is described which uses the counts of sized larvae from plankton samples to describe the development of pattern with larval age. "Patchiness" at age curves are presented for the northern anchovy (*Engraulis mordax*) and the jack mackerel (*Trachurus symmetricus*). An attempt is made to explain the dissimilarities between the curves in terms of specific differences in feeding behavior, sibling cannibalism and the development of social behavior.

INTRODUCTION

A universal charactersitic of both plant and animal populations is the non-random nature of their distributions. When mapping a population, it is often found that the spacing between organisms is more regular than that which would be due to chance alone; on the other extreme, relatively dense concentrations of organisms may be found to be surrounded by areas of relatively low densities (i.e., aggregated pattern or patchiness). Classic explanations for these observations are resource monopolization and/or territoriality in the case of uniform distributions, and environmental heterogeneity in the case of patchiness (Pielou, 1974). Social behavior may also explain patchiness in the population distribution of certain mammalian, avian, insect and fish taxa (Wilson, 1975, and numerous references cited within).

In the pelagic marine habitat, phytoplankton patchiness is probably caused by environmental discontinuities in nutrient supply, sunlight and grazing pressure. Patchiness among invertebrate and vertebrate groups is often attributed to social behavior; advantages include reduction of predation, enhancement of reproductive activities, increased efficiency of movement and population regulation (e.g., Clutter, 1969; Brock and Riffenburgh, 1960). However, there are occasions where patchiness is not so readily explained; specifically the aggregated pattern encountered when sampling fish eggs and larvae at a stage prior to the onset of social behavior. The observed patchiness of ichthyoplankton may be explained as the result of parental behavior to achieve efficient fertilization; if this were the only reason natural selection would favor those characteristics which inhibit egg dispersion and thus maximize zygote formation. One would expect convergence in egg geometry, batch size, and general spawning behavior.

Convergence is not observed: some species lay ovoid eggs while others lay spheroid eggs; some eggs have embossed patterns of ridges on their surface while others are smooth; some fish are batch spawners while others are serial spawners; some release large numbers of small yolked eggs while others release fewer but larger yolked eggs. All of these features have an effect on the dispersion of eggs and it may be that fertilization and the subsequent dispersal pattern of the young are both being optimized. I am proposing that larval patchiness does indeed contribute to survival specifically by facilitating visual contacts between larval which appear to be essential to the ontogeny of schooling behavior (Shaw, 1970; Williams and Shaw, 1971). From this viewpoint, pattern is considered one of a suite of co-evolved characters which together describe the life history of the larval phase. The patchiness of planktonic eggs and larvae is initially determined by parental spawning behavior (Smith, 1973) and the physical forces which drive oceanic diffusion. If increased social contacts between larvae contribute to their survival then spawning behavior is subject to selection, particularly with respect to the initial scale and intensity of egg patches. It follows that the intensity of egg patchiness may have evolved to complement the average diffusion conditions in the sea and that anomolous environments may inhibit or enhance the development of schooling behavior.

The positive aspects of larval patchiness are reduced by the detrimental effects of increased competition for food and, in some species, sibling cannibalism (Mayo, 1973). The pelagic larvae of various fish species, or at least groups of species, differ widely in morphology, growth rate, visual acuity, swimming ability, prey selectivity, and tendency to cannibalism. If we acknowledge the existence of density-dependent events in the larval and early juvenile stages (e.g., feeding, ontogeny of schooling, settling success for demersal fishes) then pattern must be included in the above list.

This paper presents the initial investigation of the hypothesis that patchiness is an important characteristic of larval existence. It is limited to the question: do differences exist between two species in their larval dispersion patterns and can these differences be explained by differences in other characteristics of their life history? The index used to quantify patchiness is briefly reviewed and pattern is traced, as a function of larval age, for a carangid (*Trachurus symmetricus*) and an engraulid species (*Engraulis mordax*).

QUANTIFYING PATTERN

Two classes of methods are used to reconstruct population pattern from sampling information: those that employ distance as a continuous variate and those that use numbers-per-quadrat as a discrete variate (Pielou, 1977). The first methodology relies on distance sampling to measure the spatial distribution of individuals (e.g., the distance to the nearest neighbor from randomly chosen individuals is used as a variate). The second methodology uses as a variate the number of individuals counted in a randomly chosen quadrat encompassing some finite space. When the population does not distribute itself into natural quadrats (such as in the organs of parasite hosts), distance sampling is preferred because the delimitation of artificial quadrats imposes a scale on the pattern detectable. However, distance sampling is possible only for sessile animals and plants or when a synoptic picture of the distribution of motile animals is possible. Planktonic populations are most directly sampled using quadrats where the quadrat size is defined as the volume of water captured in a bottle or filtered by a net.

The results of a survey may be presented as a histogram of numbers-per-quadrat which, in the case of an aggregated population, is skewed with a disproportionately large proportion of the organisms retained in a small number of samples. The histogram may be summarized by an estimate of the population mean and variance. Several indexes, sensitive to pattern intensity, have been derived as a function of the mean and variance. Some are affected by population density such as the variance/mean ratio, "index of clumping" (David and Moore, 1954) and "mean crowding" (Lloyd, 1967). Others are unaffected by density, such as Morista's (1959) "index of dispersion" and Lloyd's (1967) "patchiness". Density independence is an attractive feature because it allows the use of these measures to compare the pattern of populations irrespective of their abundance levels.

These indices measure the intensity of pattern but not the scale (or grain) of pattern. Intensity is defined as the extent to which local density varies from place to place and scale is the relative spatial extent over which the whole range of densities is found. The resolution of these indices (i.e., the minimum scale at which pattern intensity may be detected) is the distance traversed with an oblique plankton tow.

The index used here is Lloyd's (1967) "patchiness" which is a function of "mean crowding." Lloyd has defined mean crowding ($\overset{*}{m}$) as "the mean number per individual of other individuals in the same quadrat." Thus:

$$\overset{*}{m} = \frac{\sum_{i=1}^{Q} x_i(x_i - 1)}{\sum_{i=1}^{Q} x_i} = m + \left(\frac{\sigma^2}{m} - 1\right)$$

where the population is distributed into Q quadrats x_i is the count of organisms in the ith quadrat, σ^2 is the population variance, and m is the population mean. Thus, mean crowding ($\overset{*}{m}$) is the mean density improved by the amount that the variance to mean ratio exceeds unity. In a randomly dispersed population the variance equals the mean, and $\overset{*}{m}$ and m are also the same.

Patchiness is mean crowding standardized by the mean density:

$$\frac{\overset{*}{m}}{m} = 1 + \frac{\sigma^2 - m}{m^2}$$

and may be considered to measure how many times more crowded an average individual is relative to an individual in a population with the same mean density but randomly dispersed.

It can be shown (Hewitt, unpubl. MS) that a random removal of a fraction of the population (density independent mortality) reduces mean crowding proportionately but patchiness remains unchanged. Thus, mean crowding is something that is experienced by the individual and depends on the absolute abundance. Patchiness is a property of pattern and is independent of population density; two populations can exhibit the same degree of patchiness even though their densities differ (Pielou, 1977).

In order to arrive at a standard error for the sample estimate of population patchiness, I have assumed the underlying distribution to be negative binomial (Lloyd, 1967, Zweifel and Smith, this volume). The negative binomial distribution is specified by two parameters: the mean (m) and k (the reciprocal of k has been used as an index of patchiness, e.g. Waters, 1959, Cassie, 1962). The population variance is related to m and k:

$$\sigma^2 = m + \frac{m^2}{k}$$

Thus:

$$\frac{\overset{*}{m}}{m} = 1 + \frac{1}{k}$$

The sample estimate of patchiness is by analogy:

$$\frac{\overset{*}{x}}{\bar{x}} = 1 + \frac{1}{\hat{k}}$$

Where $\hat{k}$ is the maximum likelihood estimate of k (Bliss and Fisher, 1953). This method is particularly attractive in the case of highly contagious populations because it makes use of the entire sample distribution rather than its summary form: the mean and variance. The expression for the standard error of the sample estimate of patchiness was given by Lloyd as:

$$\text{S.E.}\left[\frac{\overset{*}{x}}{\bar{x}}\right] \cong \frac{1}{\hat{k}^2}\left[\widehat{\mathrm{var}\,(\hat{k})}\right]^{.5}$$

where var (k) is the sampling variance for k.

THE FISH

The gross morphology of the northern anchovy larva (*Engraulis mordax*) is characteristic of clupeoid fish larvae: elongate body, small fins, and a small terminal mouth (Fig. 1a). Except for the yolk-sac stage and a short period after yolk-sac absorption, growth in length is approximately linear with age over the time that the larvae are susceptible to capture (Zweifel and Lasker, 1976, Fig. 2), although Hunter (1976) has described growth over the entire larval period as curvilinear.

Northern anchovy are initially euryphagous but soon adjust their diet to the eggs, nauplii, and copepodid stages of small copepods; the size of prey eaten increases with age (Arthur, 1976). Anchovy are able to persist for up to 20 days on a euryphagous diet (Lasker et al., 1970) but growth is depressed.

In the process of feeding, a northern anchovy larva assumes a sinusoidal posture and sculls toward the prey; at a short distance the larva straightens its body, drives forward and captures the prey. If a strike is unsuccessful, repeated efforts are seldom made toward the same prey (Hunter, 1972).

Northern anchovy larvae are capable of short (0.1–0.2 sec) swimming bursts with an average speed of 15 body lengths per second but this mode of swimming behavior is increasingly rare with age. The dominant form of larval swimming, used for prey search, is a beat and glide mode similar to that of the adults (Hunter, 1972). While this behavior results in a slow speed of advance, Vlymen (1974) has calculated that it has relatively high metabolic efficiency.

The larva of the jack mackerel (*Trachurus symmetricus*) rapidly changes from an elongate shape to a deep bodied form with a large jaw structure and eyes (Fig. 1b). No clear cut distinction exists between larvae and juveniles; the larval period is considered to end at the completion of fin formation (Ahlstrom and Ball, 1954). Initial growth is slow (Theilacker, 1978) but must accelerate at a later age to a value greater than that for the anchovy because 1 year old jack mackerel are larger than 1 year old anchovy despite the fact that the jack mackerel were spawned later in the year (Wine and Knaggs, 1975; Spratt, 1975; Kramer and Smith, 1970, 1971).

The larval growth curve for jack mackerel (Fig. 2) was approximated to fit the growth of laboratory reared larvae (Theilacker, 1978; and pers. comm.) and field caught larvae aged by R. Methot using daily otolith increments. Reduction in growth rate was not observed at the end of the larval phase (Theilacker, pers. comm.) as it was for the anchovy.

Jack mackerel larvae consume larger prey as they grow and rapidly shift from naupliar to copepodid

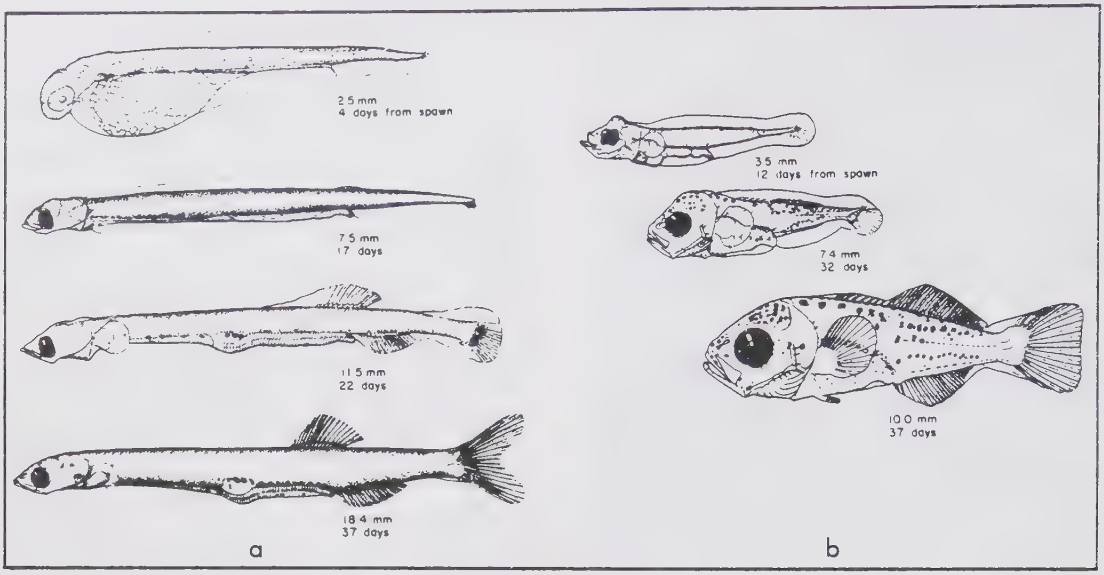

Figure 1. (a) Four developmental stages of the larva of the northern anchovy, *Engraulis mordax*. From Kramer and Ahlstrom 1968. (b) Three developmental stages of the larva of the jack mackerel, *Trachurus symmetricus*. From Ahlstrom 1969.

stages as preferred food items (Arthur, 1976). A shift to larger prey implies a shift to more rare prey because the density of food particles in the sea decreases exponentially with particle size (Sheldon and Parsons, 1967; Sheldon et al., 1972). Vlymen (1977) and Arthur (1977) described similar distributions in the coastal waters off California; a jack mackerel larva eating copepodites would find its prey 1–2 orders of magnitude less abundant than the naupliar stages eaten by anchovy larvae. Arthur (1977) also finds the different naupliar stages to have a similar type of contagious distribution whereas copepodid stages are more uniformly distributed. Jack mackerel larvae feed with a simple biting lunge and do not employ the more time consuming coil, advance, and strike mode of the anchovy.

The swimming of jack mackerel larvae has not been described although Hunter and Kimbrell (1980) has observed that a morphologically similar larva (deep, robust body) of the Pacific mackerel (*Scomber japonicus*) increases its cruising speed from 2 to 3 body lengths over the larval period. Theilacker (pers. comm.) states that jack mackerel larvae swim at a steady moderate speed and do not engage in high speed bursts as the Pacific mackerel do. On the basis of the contrast between beat and glide swimming and continuous tail beat swimming, one may expect differences to exist between the anchovy and jack mackerel in their searching ability and metabolic requirements, with the jack mackerel expending more energy to search a larger volume of water.

In contrast, the clupeoid larva swims at a slower rate, expending less energy and searches a smaller volume of water; its preferred food is smaller and therefore more common. The carangid larva eats rarer prey and must search further for it; its higher locomotor ability aids in the search for food and maintains the frequency of contacts between dispersed individuals. High larval densities may be less detrimental to the feeding success of anchovy than jack mackerel; whereas low larval densities may be less detrimental to successful school formation among jack mackerel than anchovy. Thus, it seems reasonable that the formation of dense patches of eggs and slow dispersion rates favor clupeoid larvae, while low egg densities would be more favorable to the more active larvae. Table 1 summarizes larval characteristics of the northern anchovy and the jack mackerel relevant to distribution pattern.

THE DATA

Counts of anchovy and jack mackerel larvae from the California Cooperative Oceanic Fisheries Investigations (CalCOFI) ichthyoplankton collections were examined and enumerated by size

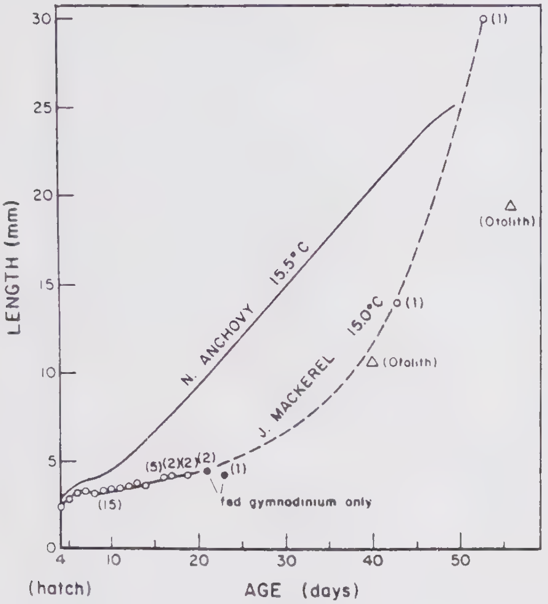

Figure 2. Larval growth curves (length at age) for the northern anchovy and the jack mackerel. Northern anchovy growth is based on the Laird-Gompertz model fit by Zweifel and Lasker (1976) and further elaborated by Zweifel and Smith ms. The growth curve for jack mackerel was fitted by eye to data on laboratory reared fish and two field caught fish; the numbers in parentheses indicate the number of fish at a given age whose length was measured; each of the first 11 points (up to 10 days age) are the average of 15 fish (Theilacker, 1978).

classes. Data was available for the anchovy for stations occupied between 1951 and 1969 and for the jack mackerel between 1961 and 1969. Because the interpretation of zero counts is ambiguous (they either represent samples drawn from outside the animal's habitat or they are true zeros resulting from the patchy character of egg and larvae distributions), only those samples which captured a larva of any size were selected. This analysis pooled sized larvae counts from 11 650 samples (out of 25 360) which were positive for any size anchovy larvae and from 1 879 samples (out of 9 459) which were positive for any size jack mackerel larvae. The two sets of samples were assumed to be representative of each species habitat and the dispersion of larvae among these samples was examined.

The decrease in mean number of larvae per sample with time (size was translated to age using the growth curves) is interpreted as the result of mortality. A crude mortality estimate, based on a linear transformation of the exponential curve, obtained an instantaneous mortality of 0.16 for the anchovy and 0.18 for the jack mackerel.

Dispersion was evident from the initial increase in positive samples even though the abundance of larvae was decreasing at a substantial rate (Fig. 3b). The proportion of positive samples for anchovy larvae increased and reached a maximum after 18 days; during this same time the cohort suffered an order of magnitude decrease in numbers. The jack mackerel achieved maximum dispersion after about 10 days and rapidly disappeared from a large portion of the samples.

Evidence for an increase in patchiness is described in Figure 3c where mean larval abundance is plotted against age. The closed squares are the mean number of larvae per sample throughout the habitat and their decline with age is the result of mortality. The open squares are the mean number of larvae per sample positive for that age larvae and are a measure of local abundance in that portion of the habitat where they are found. The mean per positive sample will decrease in response to mortality and may decrease or increase in response to dispersion or aggregation. For the anchovy the open and closed squares diverged at 18 days suggesting that the effect of mortality on local density is somewhat offset by increasing patchiness; a similar increase in patchiness is observed for the jack mackerel beginning at an earlier age.

The anchovy exhibited an initially high degree of patchiness, achieved a maximum dispersion at about 18 days and showed a rapid increase in patchiness thereafter (Fig. 4). The jack mackerel started out less patchy and achieved maximum dispersion at an earlier age.

Table 1. Summary of larval characteristics relevant to distribution pattern.

Characteristic	Northern anchovy	Jack mackerel
Swimming ability	Poorly developed	Well developed
Prey	Small size, abundant and patchy	Large size, uniformly rare
Volume of water capable of searching	Small	Large
Dispersion	Low	High
Expected contact between larvae necessary for development of schooling behavior	High	High

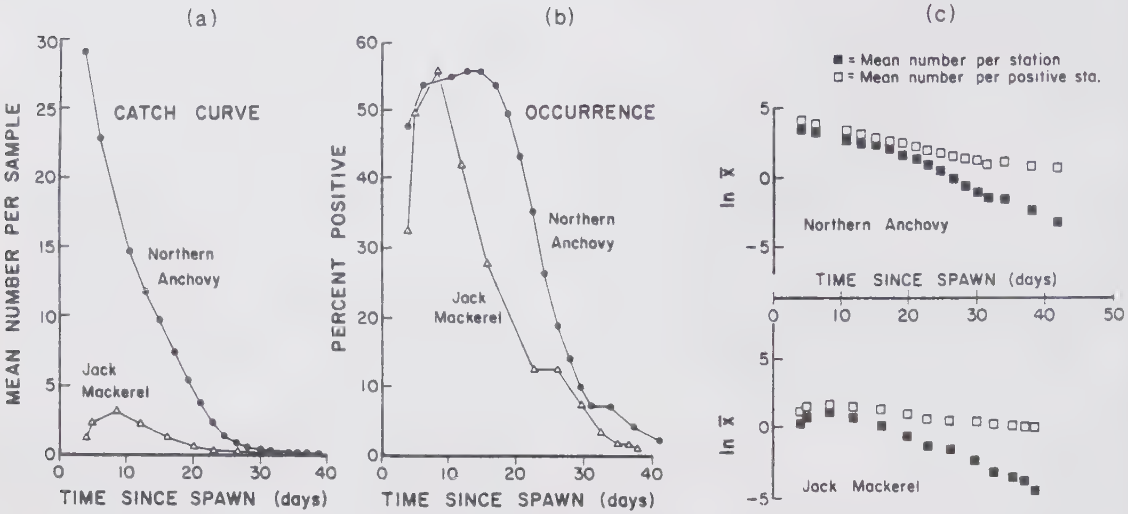

Figure 3. (a) Catch curve of larvae expressed as mean number of larvae per sample by age categories. The first two jack mackerel groups are undersampled relative to the other classes as a result of rapid growth in the yolk-sac stage and extrusion of small larvae throughout the meshes of the net. (b) The proportion of samples positive for larvae of a particular age. (c) The natural logarithms of the mean number of larvae per sample and the mean number of larvae per sample positive for larvae of a particular age. Change in the mean number per sample indexes mortality; change in the mean number per positive sample indexes patch density and is sensitive to mortality and dispersion. A divergence of the means is interpreted as evidence of increasing patchiness.

DISCUSSION

The curves described by Figure 4 were obtained from pooling data over large temporal and spatial regimes and as such represent average conditions for the period considered. Patchiness is a non-dimensional quantity best used to describe the character of pattern as a population trait rather than as perceived by the individual. The index used here is defined as a measurement of how many more times an individual is crowded relative to an individual in a randomly dispersed population of the same size. Jack mackerel larvae are never more than 1/10 as abundant as equal-aged anchovy larvae yet the development of their pattern shows a similarity to that of the anchovy. Both fish are initially patchy, disperse, and then become patchy again. The increase in patchiness may be due to a response to food gradients (Hunter and Thomas, 1974), or to uneven predator pressure, or hydrographic features, or movements observed early in the development of social behavior (Shaw, 1960, 1961; Jorne-Safriel and Shaw, 1966). Whatever the cause, patchiness maintains continued contact between larvae necessary to the integration of approach/withdraw and approach/orient behaviors. The merging of such opposing reactions has been shown to be essential to the development of schooling behavior (Williams and Shaw, 1971).

The jack mackerel was not only less abundant but less patchy than the anchovy in the early larval phase. Presumably this pattern is an evolutionary response to the relative scarcity of jack mackerel larval food. Apparently the initial intensity of patchiness was high enough to insure that the larvae were never completely dispersed to a random pattern. If complete dispersal had occurred, the larvae would have had little or no contact between them and subsequent schooling behavior would have been adversely modified (Williams and Shaw, 1971) or non-existent. Jack mackerel larvae were never significantly more patchy than anchovy larvae even though they were much less abundant. Presumably the more active larvae are capable of maintaining contact between more widely separated individuals.

The curves in Figure 4 describe the evolution of pattern for two very different larvae. They lend credence to the idea that pattern is species specific or at least specific to larval types and that pattern is important to larval events. The next phase in this work will be to determine a similar curve for a pelagic larva that does not eventually school. Patchiness will also be examined in particular years, seasons, and subportions of the habitat and then compared with the long term mean. Particular attention will be directed toward correlations with seasonal variation in

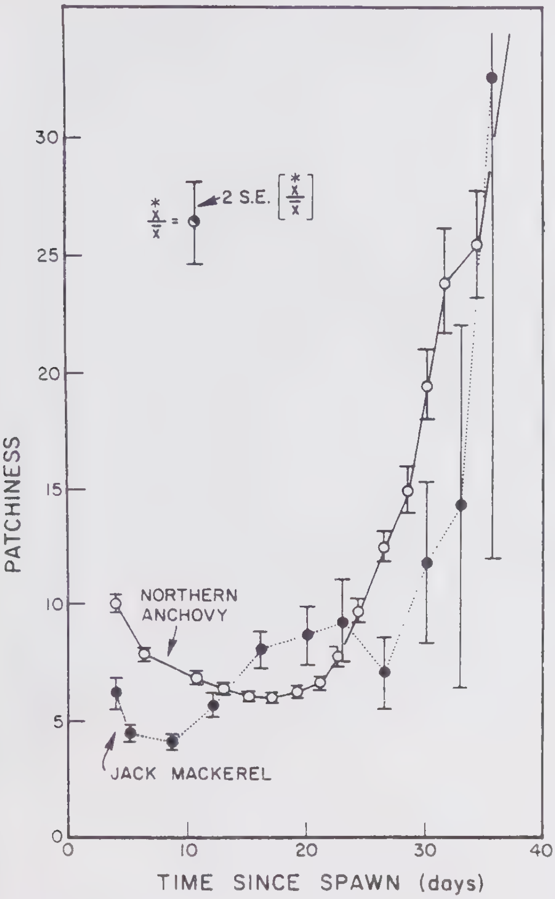

Figure 4. Lloyd's (1967) index of patchiness as a function of larval age, where patchiness measures the degree of departure from a random dispersion pattern.

spawning biology, geographic expansion (or contraction) of the spawning area, anomalies in horizontal mixing, and, finally, survival variation in the late larval, early juvenile phase.

Smith and Lasker (1978) have noted that while the anchovy population has increased approximately by an order of magnitude between 1951 and 1969, the number of large larvae has remained relatively constant. It is apparent that there must have been large variations in survival through the late larval phase to account for the increase in anchovy numbers. Abundance of older larvae yields little information as to the future success of recruitment and it may be that the important predictive factor is not how many larvae have survived but rather their dispersion pattern.

ACKNOWLEDGEMENTS

The hypothesis presented in this paper was developed as a result of conversations with Paul Smith, John Hunter, and Michael Mullin. I am indebted to them for their guidance and editorial assistance. James Zweifel provided insight into the usefulness of the negative binomial distribution, as well as technical assistance in its application.

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CREPUSCULAR AND NOCTURNAL ACTIVITIES OF CALIFORNIAN NEARSHORE FISHES, WITH CONSIDERATION OF THEIR SCOTOPIC VISUAL PIGMENTS AND THE PHOTIC ENVIRONMENT[1]

Edmund S. Hobson,[2] William N. McFarland,[3] and James R. Chess[2]

ABSTRACT

Activities in 27 of the major southern Californian nearshore fish species, with emphasis on trophic relationships, were studied between 1972 and 1975 at Santa Catalina Island. Because these fishes orient primarily by vision, they are strongly influenced by the underwater photic environment, which we define with representative spectra. We center on crepuscular and nocturnal events, but also describe daytime events for comparison.

The species that feed mostly by day include *Atherinops affinis*, *Paralabrax clathratus*, *Girella nigricans*, *Medialuna californiensis*, *Brachyistius frenatus*, *Cymatogaster aggregata*, *Damalichthys vacca*, *Embiotoca jacksoni*, *Chromis punctipinnis*, *Hypsypops rubicunda*, *Halichoeres semicinctus*, *Oxyjulis californica*, *Semicossyphus pulcher*, *Alloclinus holderi*, *Gibbonsia elegans*, *Heterostichus rostratus*, and *Coryphopterus nicholsi*. Those that feed mostly at night include *Scorpaena guttata*, *Sebastes atrovirens*, *S. serranoides* (subadult), *S. serriceps*, *Xenistius californiensis*, *Seriphus politus*, *Umbrina roncador*, and *Hyperprosopon argenteum*. Those that show no clear diurnal or nocturnal mode include *Leiocottus hirundo* and *Pleuronichthys coenosus*.

Activity patterns tend to be defined less clearly in the warm-temperate fish communities of California than in fish communities of tropical reefs. Included are the twilight patterns of transition between diurnal and nocturnal modes, which are considered to be defined by predation pressures. The lesser definition of twilight patterns in California could mean reduced crepuscular predation there, but we believe that Californian fishes, too, have evolved under severe threats from crepuscular and nocturnal predators. We suggest this is evidenced in the spectral sensitivities of their scotopic visual pigments, which cluster around 500 nm—the best position for vision during twilight and at night in Californian coastal waters.

Although the scotopic system dominates vision in dim light, the spectral sensitivities of the scotopic pigments are poorly matched to the major forms of incident light at night—moonlight and starlight. Rather, they match twilight and bioluminescence, which favor similar spectral sensitivities. We believe this benefits these fishes most on defense. The match with twilight, when the low levels of incident light shift briefly to shorter wavelengths, enhances vision during the crepuscular periods of intensified threats from predators. And the match with bioluminescence permits fishes to react to threatening moves in nocturnal predators by responding to luminescing plankton that fire in the turbulence generated by these moves.

Most fishes that live in southern Californian coastal waters orient by vision, and so are strongly influenced by the characteristics of underwater light at different times of the diel cycle. Knowing that these variations in light are accompanied by differing behavior patterns in the fishes (Hobson and Chess 1976; Ebeling and Bray 1976), we consider here circumstances during twilight and at night, when light is reduced and the fishes' scotopic (dim-light sensitive) visual systems are operating (McFarland and Munz 1975c). A later report will consider circumstances during daylight. We relate the crepuscular and nocturnal activities of the fishes and their scotopic visual pigments to the spectral composition of light in their warm-temperate habitat, and compare these relationships with the similar ties among activities, visual pigments, and light among fishes in tropical waters.

We stress trophic relationships, because we consider these the major forces shaping activity patterns and related sensory systems in these fishes. The species studied are among the more numerous and readily observed in the nearshore warm-temperate eastern Pacific Ocean. Our accounts of

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their activities cover observations over 15 yr in southern California—from San Diego north to Point Conception—but our more detailed observations, along with the light measurements and analysis of visual pigments, refer to Santa Catalina Island (lat. 33°28′ N, long. 118°29′ W), 35 km from the mainland (Figure 1). Here the water is consistently warmer and more transparent than on the adjacent mainland; during our study surface temperatures ranged between about 11° and 20° C, and underwater visibility generally exceeded 10 m. Thus, when related to comparable data collected earlier in the tropics (Hobson 1968a, 1972, 1974; Munz and McFarland 1973; McFarland and Munz 1975a), these results offer a conservative measure of differences between warm-temperate and tropical habitats.

METHODS

Determining the Spectral Composition of Submarine Sunlight

The spectral distribution of submarine light was measured with a Gamma 3000R spectroradiometer[4] mounted in an underwater housing (Munz and McFarland 1973). The instrument, fitted with a cosine receptor head and calibrated in photons per square centimeter per nanometer per second, draws a quantal irradiance spectrum. Radiance of the backlighting along a particular line of sight was measured by restricting the angle of view of the receptor head to a narrow cone (ca. 0.008 steradians). Usually radiance was determined along the zenith, horizontal, and nadir lines of sight.

Because we were interested in comparing the spectral distribution of submarine light for different water conditions and along different lines of sight, results have been normalized and are presented in terms of relative number of photons. The light levels that occur at twilight were beyond the spectroradiometer's sensitivity for measurement of spectral radiance. At twilight, therefore, spectral irradiance and not spectral radiance was measured. Irradiance data are reported in terms of absolute numbers of photons.

To facilitate comparisons, several of the spectral curves were indexed by calculating their λP_{50} values (Munz and McFarland 1973; McFarland and Munz 1975a). The λP_{50} value represents the wavelength within the visible spectrum (400-700 nm) that halves the total number of photons under a spectral curve. Because underwater light is usually homochromatic and fairly symmetrical in distribution, λP_{50} provides a useful single index to a spectrum.

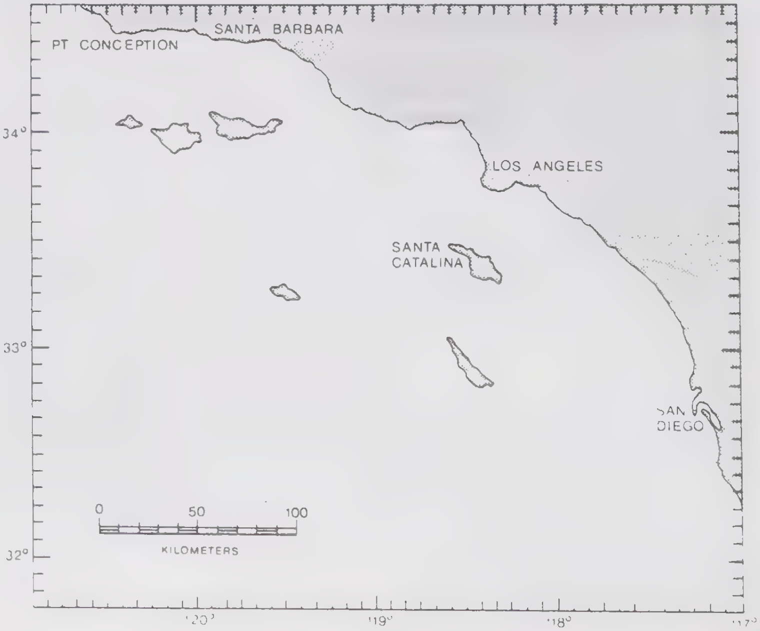

FIGURE 1.—The study area in southern California. Santa Catalina Island was the site of detailed observations, including light measurements and analysis of visual pigments in fishes.

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[4] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Determining Activity Patterns in Fishes

Our accounts of activity patterns in the fishes stem from direct underwater observations and from study of gut contents. The underwater observations were made using scuba and by snorkeling during all hours of day and night. The gut contents were from fishes speared at all hours of day and night, but primarily during late afternoon and within 2 h before first morning light—times which best distinguish diurnal and nocturnal habits. To study the gut contents, the digestive tract of each fish specimen was removed immediately after collection and preserved in a 10% formaldehyde solution. Analysis under a binocular dissecting scope was performed later in the laboratory. We note in this report only major food items that we believe might add insight to our accounts of diel activity patterns. More detailed accounts of the food habits are given elsewhere (Hobson and Chess 1976; in prep.). All measurements of fish size are of standard length (SL). Although our accounts center on crepuscular and nocturnal events, we describe enough of what happens in daylight to consider these events in the context of diel patterns.

Determining Spectral Photosensitivity of Fishes

Two techniques were used to obtain both fresh, and dark-adapted retinae from the fishes. Some of the specimens were captured alive and dark-adapted under laboratory conditions, whereas others were speared at night and immediately placed in dark containers before being returned to the laboratory for additional treatment. Spectral absorbance characteristics of the visual pigments from these retinae were determined by standard procedures. After each fish was dark-adapted, its eyes were enucleated, the retinae were removed under deep red light (Wratten #2 filter), and then frozen in 4% alum. Later the retinae were thawed, washed in triplicate, centrifuged, and the pellet extracted in 2% digitonin. Sonication of the pellet at 0° C for 1 min assisted solubilization of the visual pigment. After centrifugation, 10% by volume of saturated sodium borate and 10% by volume of 0.2 M hydroxylamine were added to the supernatant and the spectral absorbance of the extracted visual pigment recorded with a Cary 14 spectrophotometer. The method of partial bleaching (Dartnall 1952) was applied to test whether each retinal extract was homogeneous or contained more than one visual pigment. Pigment analysis was assisted by a computer program (Munz and Allen 1968) designed to test for homogeneity and also to characterize each visual pigment by estimation of the wavelength of peak absorbance (λ_{max}). Generally, the major photolabile component in a vertebrate retinal extract is the rod visual pigment, and the minor component(s) is the cone visual pigment(s) (Munz and McFarland 1975; McFarland and Munz 1975b). Thus, in each retinal extract from the Catalina samples the dominant pigment is considered the scotopic (or rod) visual pigment.

UNDERWATER PHOTIC ENVIRONMENT

Coastal waters characteristically absorb light of shorter wavelengths than do oceanic waters because they contain more dissolved organic matter. They also scatter more light due to higher concentrations of suspended particulate matter. As a result, they transmit light of longer wavelengths, and, therefore, under a midday sun appear blue-green, rather than blue like the open sea (see Jerlov 1968 for classification of water types). Starting with these well-established facts, we attempted to characterize the underwater photic environment at Santa Catalina Island.

Submarine Daylight

Midday Spectra

Essentially all submarine daylight meaningful to fishes is produced by the sun. Although photic conditions during midday are not our concern in this paper (they will be considered in a later report), midday spectra effectively illustrate some fundamental aspects of the photic environment that are needed to understand scotopic vision in fishes. In particular, midday spectra can be used to define the spectral transmission characteristics of a given water mass, and so provide means to compare the photic environment in Californian coastal waters with the photic conditions elsewhere, including comparisons of crepuscular and nocturnal circumstances between different habitats.

Californian coastal waters vary greatly in the way they transmit light, and while some of this variation is seasonal, much is shorter term and irregular. At times during our study at Santa Catalina very little suspended material was present, and underwater visibility exceeded 20 m, but at other times heavy phytoplankton blooms reduced visibility to <3 m. (We define underwater visibility as the horizontal distance over which we could see major environmental features in daylight.) Most of the time, however, conditions were intermediate between these extremes. Although our irregular observations of visibility do not permit a precise figure, we estimate that at least 70% of the time horizontal visibility in daylight was between 8 and 12 m. The images that we saw in these more typical conditions were relatively sharp—more like images seen in clear water than the relatively fuzzy images seen in turbid water.

So in characterizing the photic environment in the surface waters, we recognize three sets of conditions: 1) clear—when visibility exceeded about 15 m amid relatively small amounts of visible suspended or dissolved materials, 2) bloom—when visibility was less than about 5 m owing to dense phytoplankton, and 3) typical—the more usual condition, when circumstances were intermediate to the above. Thus, when visibility was about 20 m in July 1976, the spectral radiance showed the essential blue-greenness of the water (Figure 2: clear curve), whereas when visibility was about 3 m during a phytoplankton bloom in May 1974, the spectra showed a shift toward the yellow-green wavelengths (with $>50\%$ of the photons in the visible spectrum located between 500 and 600 nm; Figure 2: bloom curve). Under bloom conditions, therefore, the radiance was similar to that of lakes rich in plants (McFarland and Munz 1975c). The more usual intermediate condition, however, was closer to the clear than to the bloom condition (Figure 2: typical curve). Nevertheless, even under the clearest conditions encountered at Santa Catalina, the water was greener than it was under similar circumstances in a tropical lagoon (Figure 2: tropical-sea curve).

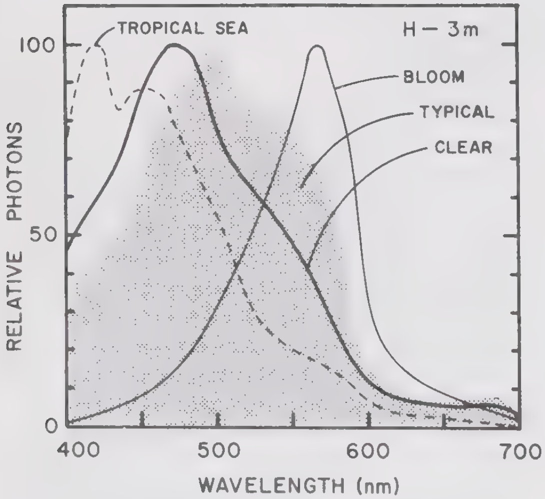

FIGURE 2.—Horizontal spectral radiance in warm-temperate coastal waters (Santa Catalina Island) under typical, bloom, and clear conditions, and in a tropical sea (Enewetak Atoll) under clear conditions. Cosine detector was 3 m below surface oriented horizontally (90° from the zenith). All values normalized, with typical condition at Santa Catalina stippled for emphasis.

The spectra depicted in Figure 2 represent a horizontal view, which effectively measures the background spacelight (or horizontal backlighting) against which the fishes studied here see most objects. At the same time we also measured downwelling and upwelling spectra, but they add nothing to the topics considered in this paper that is not illustrated by the horizontal readings. So they will be included in our later paper on photic conditions during midday.

Twilight Spectra

The broad spectrum of downwelling light in near-surface waters at Santa Catalina shifted toward the blue during twilight (Figures 3, 4), even though skylight acquires relatively more red photons at this time. Fading daylight characteristically loses photons between 550 and 700 nm more rapidly than it loses photons below 550 nm, so that as twilight progresses the proportion of photons at the shorter wavelengths steadily increases (McFarland and Munz 1975c; McFarland et al. 1979). The pattern varies in response to changing local conditions, however. For example, on 21 November 1974, events at day's end proceeded typically under a clear sky until shortly after sunset (Figure 3, top and middle panels). At this time, the sky suddenly was covered by a layer of cirrostratus clouds and immediately acquired a red-orange hue (through refraction of the sun's rays). Although we did not record atmospheric spectra at this time, an underwater spectrum recorded 10 min after sunset (Figure 3, bottom panel) was essentially flattened across the visible wavelengths. Other variations in the twilight shift to shorter wavelengths occur under differing water conditions, as exemplified by a weakening of the phenomenon during phytoplankton blooms (Figure 4). The extent of the blue shift during underwater twilight can be measured by the

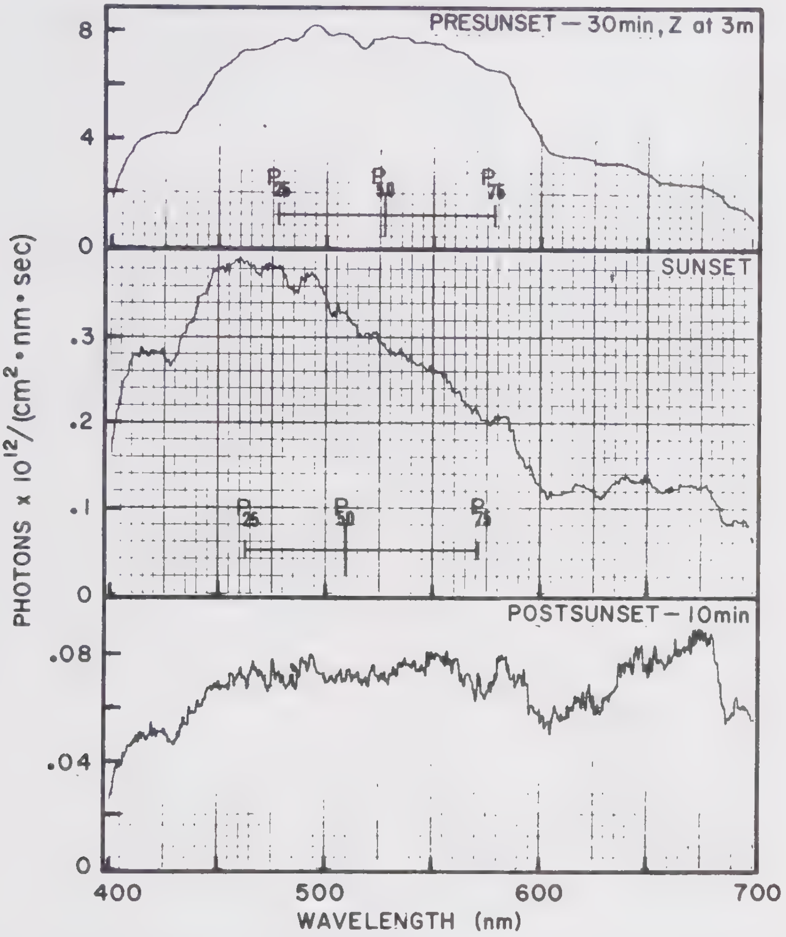

FIGURE 3.—Changes in downwelling submarine spectral irradiance through sunset near the surface at Santa Catalina Island under typical conditions. The shift toward the shorter wavelengths typical of surface waters at sunset (McFarland and Munz 1975c) is apparent in the upper and center graphs, where those wavelengths that divide the number of visible photons into equal quarters are identified by P_{25}, P_{50}, and P_{75}. The bottom graph represents the underwater spectrum when a thin layer of clouds moved over the sky at about 300 m altitude and demonstrates some of the variability that can stem from meteorological events.

changes in λP_{50}. Thus, during our observations under typical conditions, λP_{50} shifted from a presunset value of 527 to 509 nm (Figure 3), and during bloom conditions from 540 to 528 nm (Figure 4). Presumably the λP_{50} would have been closer to 500 nm had we made comparable measurements during twilight when the water was exceptionally clear.

Submarine Nightlight

Moonlight, starlight, and bioluminescence are the major forms of submarine nightlight meaningful to fishes. We did not measure these during the present study, but data available in the literature permit a comparison of the spectra each would be expected to produce in water like that typical of Santa Catalina (Figure 5). The influence of moonlight and starlight on activities in fishes and other aquatic predators has been discussed (e.g., Hobson 1965, 1966). This report considers the role of bioluminescent emissions of epipelagic plankton in predator-prey relationships.

Epipelagic bioluminescent plankton, especially dinoflagellates, are widespread in most neritic and oceanic seas (Tett and Kelley 1973). Sailing narratives and logbooks of open water mariners are replete with descriptions of the "phosphorescent

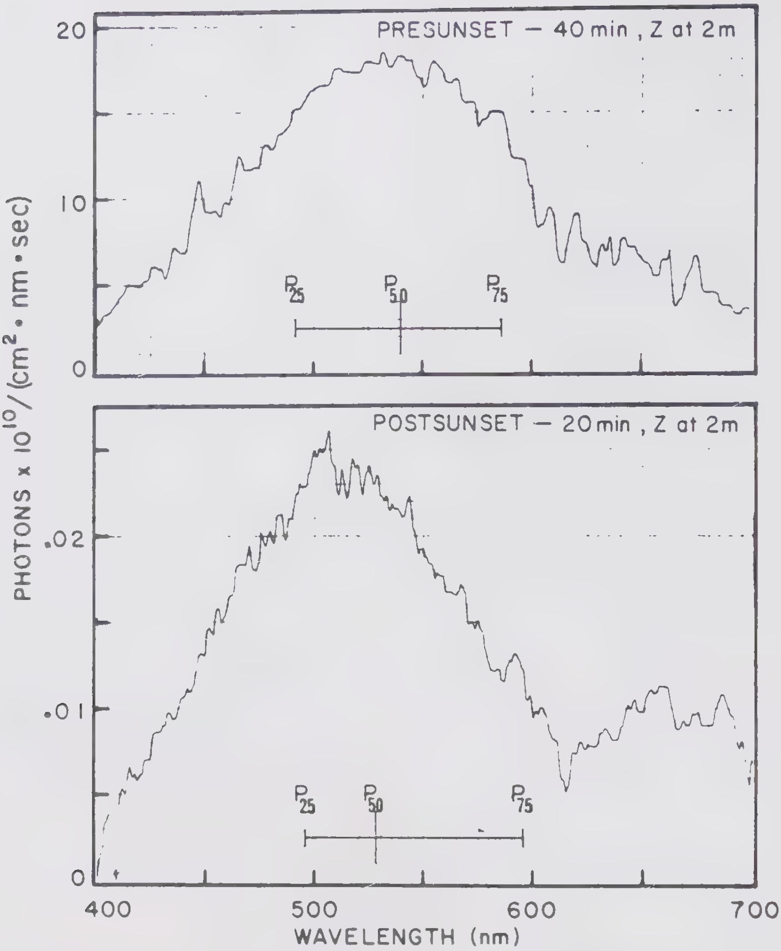

FIGURE 4.—Changes in downwelling submarine light through sunset near the surface at Santa Catalina Island during a phytoplankton bloom. Although there is relatively less blue light under these conditions, a blue shift at and following sunset is nonetheless evident when compared with daylight under bloom conditions (Figure 2). P_{25}, P_{50}, and P_{75} identify those wavelengths that divide the number of visible photons into equal quarters.

fire" of the ship's wake, the luminescent shroud about porpoises running before the bow, and the showers of sparks that trail fishes dashing below the hull. At Santa Catalina Island, bioluminescence from plankton was visible in the water at all times of the year, more so at some times than at others.

Most marine bioluminescent plankton emit light in the blue region of the spectrum (Tett and Kelley 1973). For example, light from *Gonyaulax polyedra* and *Noctiluca miliaris* (which is representative of most dinoflagellates) peaks near 475 nm, and more than half of the photons are emitted below 500 nm (Hastings and Sweeney 1957; Nicol 1958). Because of the skewed emission spectra from these organisms (Figure 6), however, fishes close to the luminescent source would absorb more photons with visual pigments that have λ_{max} values nearer 490 nm than 475 nm.

In any event, the spectral quality of bioluminescence received by the fishes is modified by two variables—distance the fishes are from the light's source, and clarity of the intervening water. Because the water more effectively absorbs the longer than the shorter wavelengths, a fish farther from a target in clear water will receive relatively more photons at the shorter wavelengths (Figure 6, upper panel). Water clarity, however, has an

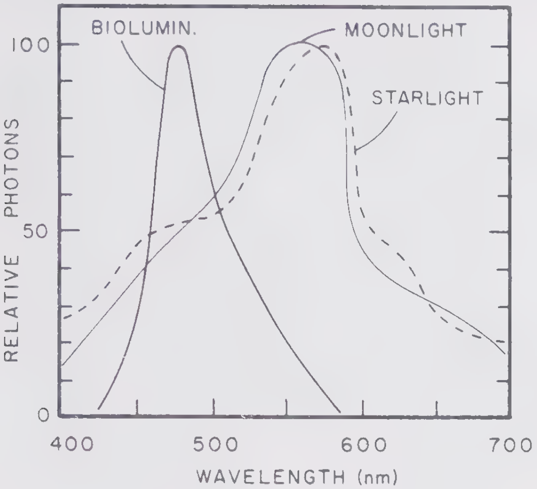

FIGURE 5.—Underwater spectral distributions of moonlight, starlight, and bioluminescence. Values for bioluminescence are for *Noctiluca miliaris*, as given by Nicol (1958), at zero range. Values for moonlight and starlight, based on measurements in Munz and McFarland (1977), are for downwelling light at zero range from a flat spectral reflector at a depth of 3 m in water equivalent to typical conditions at Santa Catalina Island (Jerlov 1968, Coastal Type 1).

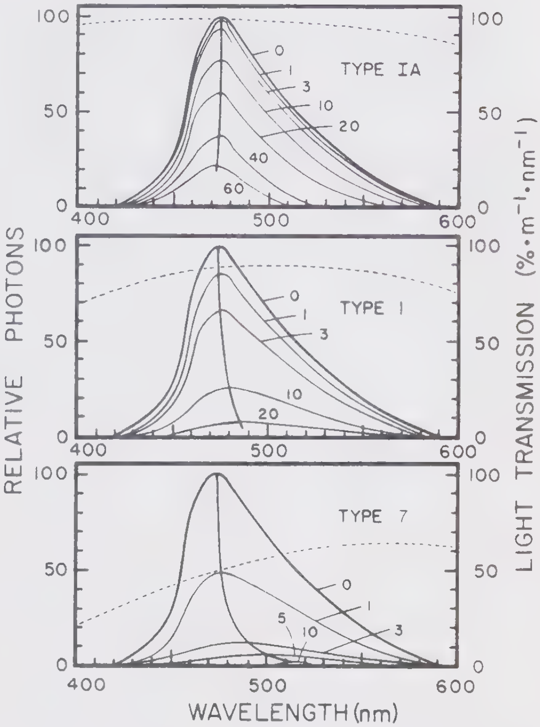

FIGURE 6.—Attenuation and spectral distribution of light emitted by *Noctiluca miliaris* over distance in water of differing clarities. The three panels of the figure each represent a different water type (clarity), as defined by Jerlov (1968): Type 1A (upper) is equivalent to clear tropical seas; Coastal Type 1 (middle) is equivalent to typical conditions at Santa Catalina Island; and Coastal Type 7 (lower) is equivalent to conditions of heavy phytoplankton bloom at Santa Catalina. The heavy outer curve in each panel represents the light emitted by *N. miliaris* (left axes) at zero range, and so is the same in each water type. The inner curves in each panel represent relative attenuation of light at distances (in meters) indicated by the accompanying numbers. The broken line in each panel represents the transmission values/meter (right axes) for that water type, as given by Jerlov (1968).

even greater effect than distance on the attenuation and spectral modification of submarine light. In the typical water we encountered at Santa Catalina, for example, there was a fairly high transmission of light between 425 and 575 nm. As light travels from a source like *N. miliaris* under these conditions its radiance attenuates slowly and its spectrum shifts only slightly (Figure 6, middle panel). On the other hand, as the same light travels through water heavily loaded with phytoplankton it attenuates rapidly and there is a marked and continuous spectral shift toward the green (Figure 6, lower panel).

ACTIVITY PATTERNS AND VISUAL PIGMENTS IN FISHES

Because the photic environment contrasts sharply between day and night, those visually orienting fishes that are adapted to diurnal conditions should be less suited to feed after dark, while those adapted to nocturnal conditions should be less suited to feed by day. This expectation has been supported in studies of temperate species, both marine (Hobson and Chess 1976; Ebeling and Bray 1976) and freshwater (Emery 1973; Helfman 1979), just as it has in studies of marine fishes in the tropics (Hobson 1965, 1968a, 1972, 1974, 1975; Starck and Davis 1966; Collette and Talbot 1972; Smith and Tyler 1972; Vivien 1973). Thus, in considering the impact of diel variations in the photic environment it is meaningful to distinguish diurnal and nocturnal species, even though some nearshore fishes feed at all hours—many by changing their food or tactics between day and night, e.g., the serranids *Epinephelus labriformis* in the Gulf of California (Hobson 1968a) and *E. merra* in the Indian Ocean (Harmelin-Vivien and Bouchon 1976) and the mullid *Parupeneus bifasciatus* in Hawaii (Hobson 1974).

We consider 27 of the most abundant fish species in the nearshore waters at Santa Catalina Island, describing what each does during twilight and at night, and noting the wavelengths of light to which the scotopic system of each is most sensitive (λ_{max}). In examining the retinae from the fishes, we noted whether the visual pigments were homogeneous. Significantly, there were no secondary pigments in 12 species and only a trace in 5. Secondary pigments, which presumably are cone pigments (Munz and McFarland 1975), were present in 10 species and abundant in only 3. The data are given below, grouped according to that segment of the diel cycle when the species obtains most of its food. It is important that we observed only slight variation in the λ_{max} of any one species.

Fishes That Feed Primarily by Day

Some of the fishes that feed primarily by day are known to be inactive at night, but evidence of nocturnal inactivity remains lacking for others, and still others are known to feed routinely after dark. The predominantly diurnal Californian fishes considered in this paper, along with certain of their visual characteristics, are listed in Table 1. The following accounts of diel activities emphasize crepuscular and nocturnal habits.

TABLE 1.—Some southern Californian marine fishes that feed primarily by day, with the spectral absorbance maximum (λ_{max}) of pigments extracted from their retinae.

Family and species	λ_{max} ±95% C.I.	*N*	Other pigments[1]
Atherinidae:			
Atherinops affinis[2]	505.8	2	0
Serranidae:			
Paralabrax clathratus[2]	498.8±2.0	4	+
Kyphosidae:			
Girella nigricans	498.3±1.0	3	0
Medialuna californiensis	496.9	2	+
Embiotocidae:			
Brachyistius frenatus	500.9±0.5	3	0
Cymatogaster aggregata	500.4±4.0	3	+
Damalichthys vacca	500.9	2	+
Embiotoca jacksoni[2]	500.8	2	+
Pomacentridae:			
Chromis punctipinnis[2]	496.1	1	+
Hypsypops rubicunda	496.3±0.1	3	0
Labridae:			
Halichoeres semicinctus[3]	513.2±7.4	3	++
Oxyjulis californica[3]	511.8	1	++
Semicossyphus pulcher[2]	496.7±3.5	3	++
Clinidae:			
Alloclinus holderi	496.5	2	0
Gibbonsia elegans	499.7±8.9	3	+
Heterostichus rostratus	499.7±2.0	4	T
Gobiidae:			
Coryphopterus nicholsi[2]	497.9	1	0
Mean[4]	499.1		
Range[4]	496.1-505.8		

[1] Other than the primary pigment: 0 = none; T = trace; + = <10%; ++ = >10%

[2] Visual pigments for these species were also studied by Munz (1957, 1958b, c, 1964). He reported similar λ_{max} values for all but *E. jacksoni*, which he listed (Munz 1958b) as 506 nm. The difference can be attributed to varying amounts of secondary pigments in his extracts, which can bias the λ_{max} estimates if not taken into account.

[3] Visual pigments in these species are porphyropsins, which are based on the aldehyde of Vitamin A_2. Pigments in all other species are rhodopsins, which are based on the aldehyde of Vitamin A_1.

[4] *Halichoeres semicinctus* and *O. californica* excluded owing to basic differences in their pigments (see footnote 3, above).

Atherinidae: *Atherinops affinis*

The topsmelt aggregates by day in the surface waters close to kelp forests, but at night most larger individuals move away from the kelp and disperse close beneath the water's surface over adjacent deeper water. At first we suspected these larger individuals might feed after dark. Their movements are similar to those of tropical Pacific atherinids of the genus *Pranesus*, which are known to be nocturnal feeders (Hobson and Chess 1973; Hobson 1974; Major 1977), and nocturnal habits are widespread in other planktivorous atherinids, including *Allanetta harringtonensis* in the tropical Atlantic Ocean (Starck and Davis 1966). Furthermore, we have often seen *Atherinops affinis* feed at night next to illuminated piers, although we consider this an artificial situation.

Despite the evidence of nocturnal feeding in other atherinids, however, our suspicions concerning *A. affinis* were contradicted by examination of gut contents. Of 22 individuals (129-219 mm SL, $\bar{x}$ = 168.8) collected at dawn as they reassembled in schools along the outer edge of kelp forests, 19 were empty, 2 contained just a few fish scales, and 1 contained calanoids and cyphonautes larvae that appeared recently ingested—probably since sunrise that morning. At least some of the smaller *A. affinis* remain close to the kelp at night, but there is little evidence that they feed during that period. Of 10 (82-160 mm SL, $\bar{x}$ = 102.4) collected close to kelp during the hour before dawn, 9 were empty. The one with food, however, contained three gammarids and one isopod that obviously had been taken at night. In contrast, there is ample evidence that *A. affinis* feeds intensively during the day. We routinely observed this species feeding in the surface waters during all daylight hours, and only 1 of 10 (126-190 mm SL, $\bar{x}$ = 158.6) collected from a large aggregation during midafternoon lacked food in its gut; the other 9 contained $\bar{x}$ = 1,325 prey items, mostly cladocerans and copepods.

Serranidae: *Paralabrax clathratus*

The kelp bass progresses through three major ontogenetic phases based on trophic relationships. The first phase includes juveniles up to about 65 mm SL that feed primarily on zooplankton during the day and pass the night sheltered amid vegetation. The third phase includes the largest individuals—those exceeding about 165 mm SL—which are increasingly piscivorous with growth and may be primarily crepuscular (although limitations in our data leave the feeding chronology at this larger size in question).

In this paper we consider individuals representing the second phase—subadult fish between 65 and 165 mm SL. Individuals of this size feed mostly on crustaceans that live on or close to a substrate by day and swim in the water column after dark, including certain gammarid and caprellid amphipods, isopods, cumaceans, mysids, and carideans. The subadult *P. clathratus* capture these crustaceans mainly by day close to benthic cover. Most subadult *P. clathratus* do not feed at night. Only 42% (13 of 31, 72-163 mm SL, $\bar{x}$ = 110.3) of those collected during the hour before sunrise contained prey, whereas there was prey in 96% (51 of 53, 68-153 mm SL, $\bar{x}$ = 107.9) of those collected during the afternoon.

Whether or not the subadult *P. clathratus* feeds at night, however, seems related to their location. Most of them are amid rocks and vegetation at night, just as during the day, and here they seem to feed little, if at all. Of 16 (95-146 mm SL, $\bar{x}$ = 108.6) collected in these surroundings during the hour before dawn, only 1 (6%) had food in its stomach (a moderately digested caridean). Nocturnal feeding in subadult *P. clathratus* seems to occur mostly in those individuals that move after dark out over open sand (Figure 7)—a habitat only infrequently occupied by them during the day. Of the 16 (72-148 mm SL, $\bar{x}$ = 97.4) collected in such places during the hour before dawn 12 (75%) contained food, much of it fresh. Major prey were the cumacean *Cyclaspis nubila* (4 mm), the gammarids *Ampelisca cristata* (3-4 mm) and *Amphideutopus oculatus* (2-3 mm), and the caprellid *Caprella californica* (6-8 mm)—all species that are active on or close above the sand at night. Clearly, the nocturnal move over the sand is a well established feeding pattern in subadult *P. clathratus*. Nevertheless, even under these special circumstances predatory success after dark seems limited. Among specimens from open sand at night the stomachs containing food averaged only 30% full, compared with 66% full for specimens from a wide range of diurnal circumstances.

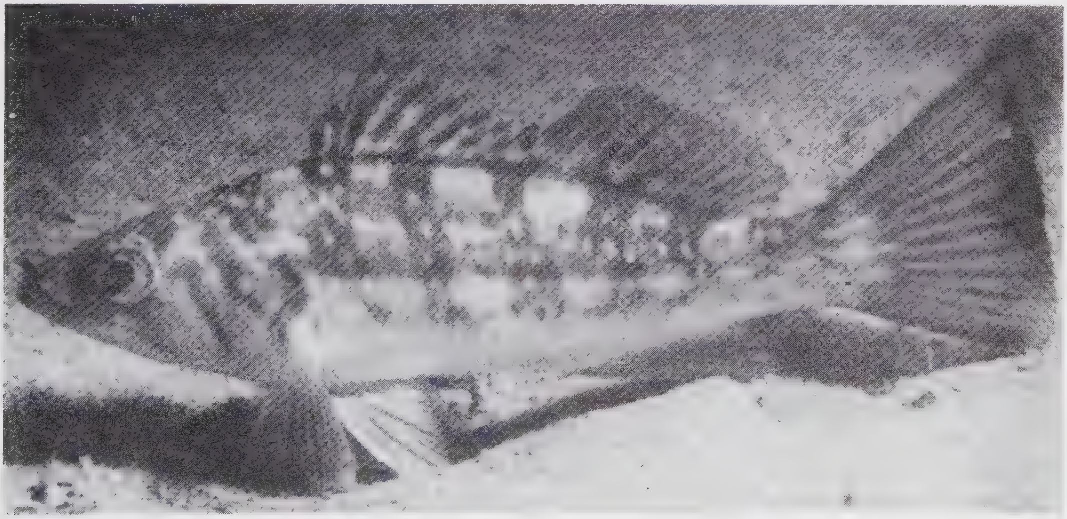

FIGURE 7.—A subadult *Paralabrax clathratus*, about 150 mm SL, alert on open sand at night. Some individuals of this size feed under these circumstances even while larger and smaller conspecifics are inactive close to rocks and algae. Apparently the sand reflects enough moonlight and starlight to permit some predominantly diurnal fishes to feed in these surroundings at night.

Kyphosidae: *Girella nigricans*

The opaleye does not seem to feed extensively at night, although our limited observations on this point are somewhat ambiguous. This rather tenuous opinion rests heavily on two points. First, the species feeds largely on algae, and various organisms that live on algae—a diet generally indicative of diurnal feeding (Hobson 1965, 1974; Vivien 1973). Second, kyphosids generally have been found to feed by day (e.g., Randall 1967). On the other hand, observations of kyphosids at night have indicated a variable condition. *Kyphosus incisor* reportedly rests "...in sheltered, though not confined, locations on the reef-top" in the Florida Keys (Starck and Davis 1966), and *K. elegans* has been noted to behave similarly in the Gulf of California (E. S. Hobson unpubl. obs.). But *K. elegans*, at least, is alert in these shelters, and *K. cinerascens* in Hawaii not only swims above the reef at night, but may feed at this time as well (Hobson 1974). The presence of *G. nigricans* "...in holes or on the bottom..." at night led Ebeling and Bray (1976) to consider it diurnal. We agree with them even though we frequently saw this species swimming in the water column after dark, especially in the kelp forest.

Limited study of gut contents suggest reduced feeding in some *G. nigricans* at night. One (201 mm) sampled among the rocks during the hour before sunrise had an empty stomach, but the stomach of another (264 mm) that was swimming above the bottom at this time was 20% full. Sixty-seven percent of the gut contents in this second individual consisted of motile animals, including gammarids, caprellids, carideans, and the gastropod *Tricolia* sp., whereas only 10% consisted of algae. This material, much of it fresh, differed sharply from that in gut contents of individuals that had been feeding by day. Benthic algae constituted 81% of the material in all 11 individuals (173-255 mm SL, $\bar{x}$ = 206) that were collected during the afternoon, and whose stomachs averaged 75% full; essentially all other items in these individuals were sessile organisms that encrust, or live attached to, algae—principally bryozoans and hydroids.

Kyphosidae: *Medialuna californiensis*

We consider the halfmoon primarily diurnal for essentially the same tenuous reasons that led us to this conclusion for *G. nigricans*: many of its close relatives reportedly are diurnal, as documented above, and it feeds heavily on plants (Limbaugh 1955; Quast 1968), a diet widely associated with diurnal foraging. Furthermore, we saw *M. californiensis*, like *G. nigricans*, in the water column in far fewer numbers at night than during the day. But although we saw *G. nigricans* in larger numbers close to rocky substrata at night, we saw *M. californiensis*, which was exceptionally numerous in the kelp forests by day, only in sharply reduced numbers there after dark. Reporting a similar situation in a kelp forest at Santa Barbara, Ebeling and Bray (1976) observed about half as many *M. californiensis* on their transect line at night as during the day. They summarized their nocturnal observations by stating that this species "...often appeared to be more sensitive to our presence than were individuals of other species near the bottom, and we cannot deny the possibility that *Medialuna* feeds at night." Leading to much the same position, our study of gut contents from 14 specimens (146-243 mm SL, $\bar{x}$ = 196) collected during the afternoon (Hobson and Chess in prep.) shows that this largely herbivorous species unquestionably feeds by day, but leaves unanswered whether or not it also feeds at night.

Embiotocidae: *Brachyistius frenatus*

Although the kelp perch is basically diurnal throughout life, this characteristic can be somewhat variable. When less than about 100 mm SL it feeds primarily on zooplankters in the water column, and as it grows larger it increasingly turns to tiny prey—mostly crustaceans—that it picks from vegetation (Hobson and Chess 1976). At night it occurs in most of the same places that it occupies by day, but is more numerous in midwater aggregations fully exposed along the outer edges of the kelp forests (Hobson and Chess 1976). Describing the nocturnal condition of this species, Bray and Ebeling (1975) noticed that it "...tended to hang motionlessly along the kelp stipes or even in open water" and added that it was "...quiescent at night and easily caught with a small hand net...." They concluded that *B. frenatus* feeds "...mostly, if not exclusively, during the day"—an opinion based on study of gut contents from specimens collected every 2 h throughout the night. But Hobson and Chess (1976) reported that while *B. frenatus* is primarily diurnal, larger individuals also feed to a limited extent at night. In addition to the data presented in that paper, all of which involved specimens <100 mm long, 6 of 14 (102-114 mm SL, $\bar{x}$ = 106.8) collected during the hour before dawn contained prey, many of them fresh. The major nocturnal prey, which included the gammarid *Batea transversa* (2-4 mm), the caprellid *Caprella californica* (8-14 mm), and the isopod *Paracercies cordata* (1-6 mm), were organisms that rise into the water column at night. We believe these prey were captured in the water column because most were in fish that had been aggregated in midwater outside the seaward edge of a kelp forest. Perhaps Bray and Ebeling (1975) found no evidence of nocturnal feeding because their sample comprised mostly smaller fish. Significantly, the major organisms apparently taken in the water column at night include the same species picked from the surface of algae by day.

Embiotocidae: *Cymatogaster aggregata*

The shiner perch, which is even more variable in its diel behavior than *Brachyistius frenatus*, has two basic feeding modes: it captures zooplankton, mostly crustaceans, in the water column, and it captures organisms, again mostly crustaceans, that are in, on, or close above a sandy bottom. The planktivorous habit predominates among individuals smaller than about 65 mm SL and continues to be important throughout life, whereas feeding on sand-dwelling forms becomes increasingly important to individuals >65 mm SL until it predominates among the largest individuals. The planktivorous habit is diurnal, whereas feeding on or close to a sandy bottom occurs during both day and night, but mostly at night.

Thus, the small juveniles are primarily day feeders: of 23 (53-64 mm SL, $\bar{x}$ = 58.2) collected during the afternoon, 12 (53%) contained food, the major items being zooplankters (mostly copepods). Only two (12%) also included prey that may have been taken from the seafloor (gammarid fragments). In comparison, only 2 of 17 (37-64 mm SL, $\bar{x}$ = 46.5) collected during the hour before dawn contained food: one (58 mm) contained just a few cumacean fragments, but the other (54 mm) contained a variety of sand-dwelling crustaceans, some fresh, including the cumacean *Cyclaspis nubila* (2-4 mm), the gammarid *Acuminodeutopus heteruropus* (1-2 mm), and the tanaid *Leptochelia dubia* (2-4 mm), along with sand.

The changes in food habits that appear among individuals >65 mm SL were similarly defined. Of 34 (67-110 mm SL, $\bar{x}$ = 91.8) collected during the afternoon, 27 (79%) contained food presumably taken by day: 19 (70%) of these had fed exclusively on zooplankton (primarily calanoid and cyclopoid copepods and cladocerans), 4 (15%) had taken only sand-dwellers (primarily tanaids and gammarids), and 4 (15%) had fed on both zooplankton and sand-dwellers in large numbers (combinations of the above forms, with the two types sharply separated in the guts). In comparison, of 46 (66-120 mm SL, $\bar{x}$ = 85.9) collected during the hour before dawn, 37 (80%) contained prey, many fresh, that appeared for the most part to have been taken at night. Significantly, all these prey were sand-dwellers, the major forms being the cumacean *Cyclaspis nubila* (2-4 mm), the gammarids *Acuminodeutopus heteruropus* (1-2 mm) and *Ampelisca christata* (2-4 mm), the tanaid *Leptochelia dubia* (3-4 mm), and the ostracod *Euphilomedes carcharondonta* (1-2 mm), along with sand.

Embiotocidae: *Damalichthys vacca* and *Embiotoca jacksoni*

Damalichthys vacca, the pile perch, and *E. jacksoni*, the black perch, both appear to be strictly diurnal feeders. During daytime, adults of *D. vacca* feed primarily on mollusks and other heavily shelled prey, whereas adults of *E. jacksoni* take an exceptionally wide variety of benthic organisms, including polychaetes, mollusks, gammarids, caprellids, isopods, and mysids (Limbaugh 1955; Quast 1968). At night we observed both species hovering close to the seafloor, generally in exposed positions. On the other hand, Ebeling and Bray (1976) reported *D. vacca* "... scattered in the water column at night." That neither species feeds after dark is evidenced by the absence of fresh food in their guts at that time (Ebeling and Bray 1976).

Pomacentridae: *Hypsypops rubicunda* and *Chromis punctipinnis*

Although the Californian pomacentrids—*H. rubicunda*, the garibaldi, and *C. punctipinnis*, the blacksmith—are strictly diurnal fishes that remain relatively inactive in their nocturnal shelters, they nevertheless remain alert throughout the night. *Hypsypops rubicunda*, in fact, often appears restless as it moves in its shelter place. This species is solitary during both day and night, and its nocturnal shelter is a specific hole or crevice in the well-defined territory that also includes its diurnal foraging area (Clarke 1970). In contrast, *C. punctipinnis* is highly gregarious during both day and night, and often individuals crowd nocturnal shelters among the rocks. When its nocturnal resting places are far from its diurnal feeding grounds, *C. punctipinnis* migrates between the two locations during twilight in prominent processions (Hobson and Chess 1976). These migrations tend to be better defined in the evening than in the morning. At times evening migrations began up to 30 min or more before sunset, while at other times they were not evident until about sunset. Generally, however, the migrations peaked from shortly before sunset until about 15 min after, and then continued at greatly reduced levels for another 10 min or so before ending.

Chromis punctipinnis is among the most numerous species on many nearshore reefs in southern California (Limbaugh 1955; Quast 1968), and in some places apparently there is insufficient rocky shelter to accommodate at night the vast numbers that forage in the water column by day. In such places excess individuals sometimes cluster after dark in dense numbers on the sand next to the reef. Occasionally *C. punctipinnis* is in the water column at night, but does not seem to feed at this time. This is attested by the empty stomachs of all 11 specimens examined from predawn collections by Hobson and Chess (1976).

Labridae: *Oxyjulis californica*, *Halichoeres semicinctus*, and *Semicossyphus pulcher*

The Californian labrids are so obviously quiescent at night that we have no doubt that, like tropical labrids (Hobson 1965, 1974), they do not feed at this time. Also, like their tropical relatives, they follow precise patterns when shifting between diurnal and nocturnal modes (Hobson 1972; Domm and Domm 1973). *Oxyjulis californica*, the señorita, buries in the sand at nightfall (Herald 1961), a habit also attributed to *H. semicinctus*, the rock wrasse, by Limbaugh (1955), who noted that this species "sleeps buried with head protruding." Feder et al. (1974) repeated this statement, as did Fitch and Lavenberg (1975), who reported that it also "burrows between or under rocks to escape predators or to sleep." We found that *H. semicinctus* consistently took nocturnal shelter amid low benthic algae (from which it often was unintentionally flushed by our nocturnal activities). Both *O. californica* and *H. semicinctus* were consistent in timing their descent to shelter in the evening, and their rise into the water the next morning. Data on the timing of these events were collected during 1973 and 1974 at Fisherman's Cove, Santa Catalina Island, in a sand-bottomed habitat dominated by the low brown alga *Dictyopteris zonaroides*. The last *O. californica* seen entering the sand on four evenings at this site slipped from view 11-22, $\bar{x}$ = 16.8, min after sunset, which agrees with Bray and Ebeling (1975), who on three occasions observed this species entering sand and rubble "About 15 min after sunset...." The first *O. californica* seen here on 11 mornings appeared 11-22, $\bar{x}$ = 15.8, min before sunrise. During the same period at this site the last *H. semicinctus* seen taking cover on six evenings disappeared 20-24, $\bar{x}$ = 22.0, min after sunset, and the first to appear on 10 mornings emerged 18-25, $\bar{x}$ = 22.8, min before sunrise. It may be significant that *H. semicinctus*, which grows to a larger size, tended to be active later in the evening and earlier in the morning. Among diurnal fishes on tropical reefs, the larger individuals tend to retire later and rise earlier (Hobson 1972). Comparable data are lacking for *S. pulcher*, the sheephead (the largest of the three Californian labrids), even though this species was numerous at the observation site during the day. *Semicossyphus pulcher* shelters among rocks at night (Hobson 1968b), and probably because the observation site lacked rocks, this species left the area sometime before going under cover. On 4 evenings the last *S. pulcher* departed the observation site 10-21, $\bar{x}$ = 18.0, min after sunset, and on 11 mornings the first to return arrived 11-24, $\bar{x}$ = 17.0, min before sunrise. On just one evening, in a nearby rocky area where the species found shelter, the last active *S. pulcher* was seen 30 min after sunset.

Because *S. pulcher* rested in distinctive shelters and was visible throughout the night (Figure 8), it offered the best opportunity to investigate consistency in resting places among individuals. Reportedly, at least some tropical wrasses return each evening to specific resting sites (Winn and Bardach 1960; Starck and Davis 1966; Hobson 1972). So the resting places of nine *S. pulcher* were located at midnight during November 1973, and then revisited at the same hour once each week for 3 wk. On the first return only two of the nine positions were occupied, No. 3 and No. 5—both by what appeared to be the same individuals that had been there before. On the second return, again only two positions were occupied: No. 5 seemed to

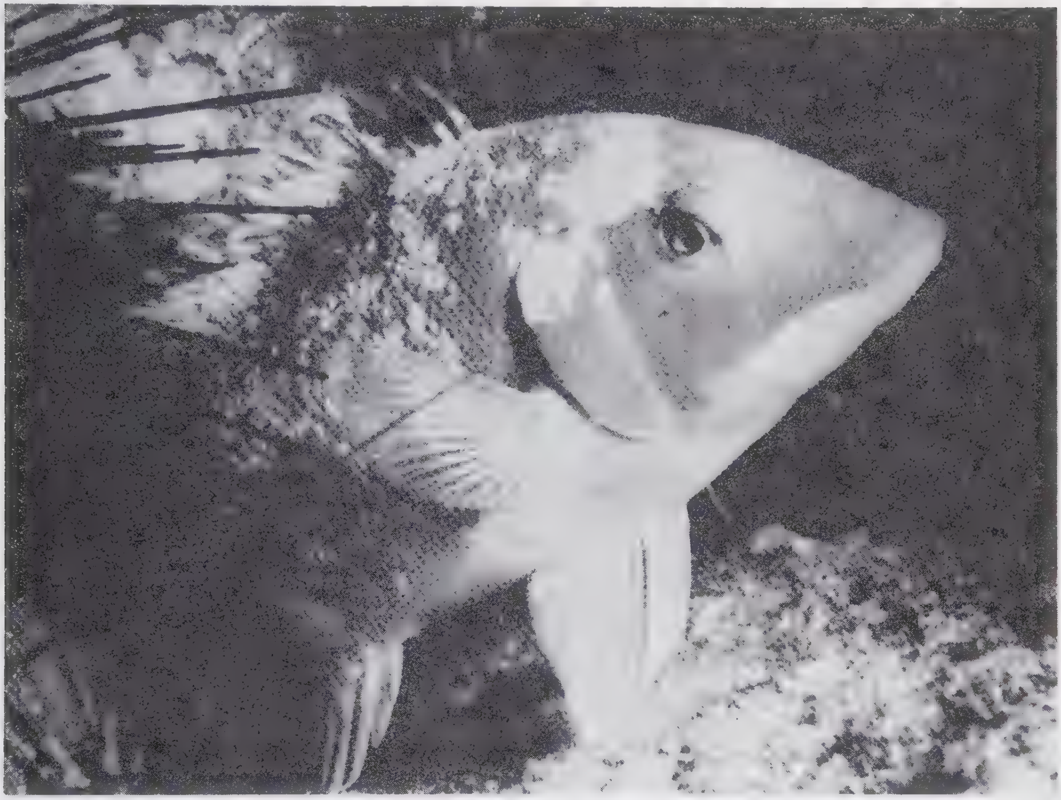

FIGURE 8.—A female *Semicossyphus pulcher* at rest on the seafloor at night, showing the typical pattern of its nocturnal hues. Its exposed position is common in this and many other nocturnally resting diurnal fishes in California.

harbor the same fish as before, but this time position No. 1 contained a small individual not seen before. On the final return, position No. 5 once more was occupied by what seemed to be the same fish. Again, just one other position was filled—No. 6, which harbored the fish seen in position No. 9 on the first night (recognized by a notch in its dorsal fin), but which had gone unseen since then. Thus, only one position, No. 5, sheltered a fish each time. And contrary to what one might expect, of the nine positions, No. 5 offered the least cover. It was simply a shallow depression on the reeftop where the resting fish was largely exposed, and certainly would not seem an effective shelter.

Clinidae: *Alloclinus holderi*, *Gibbonsia elegans*, and *Heterostichus rostratus*

The three Californian clinids studied here—*A. holderi*, the island kelpfish; *G. elegans*, the spotted kelpfish; and *H. rostratus*, the giant kelpfish—are known to feed regularly by day, based on fresh food in specimens collected during the afternoon (Hobson and Chess in prep.). But it is difficult to determine relative activity in these highly cryptic fishes because they move so infrequently and, therefore, often go unnoticed even when fully exposed. Both *A. holderi*, which sits on rocks, and *G. elegans*, which sits amid benthic algae, retire to shelter at nightfall, as do various tropical clinids (Starck and Davis 1966; Smith and Tyler 1972). *Heterostichus rostratus*, on the other hand, often hovers among columns of giant kelp during both day and night (Figure 9). Our data comparing relative feeding activity in *H. rostratus* between day and night are limited, but indicate that daytime feeding predominates. The one individual (184 mm) collected during the hour before sunrise

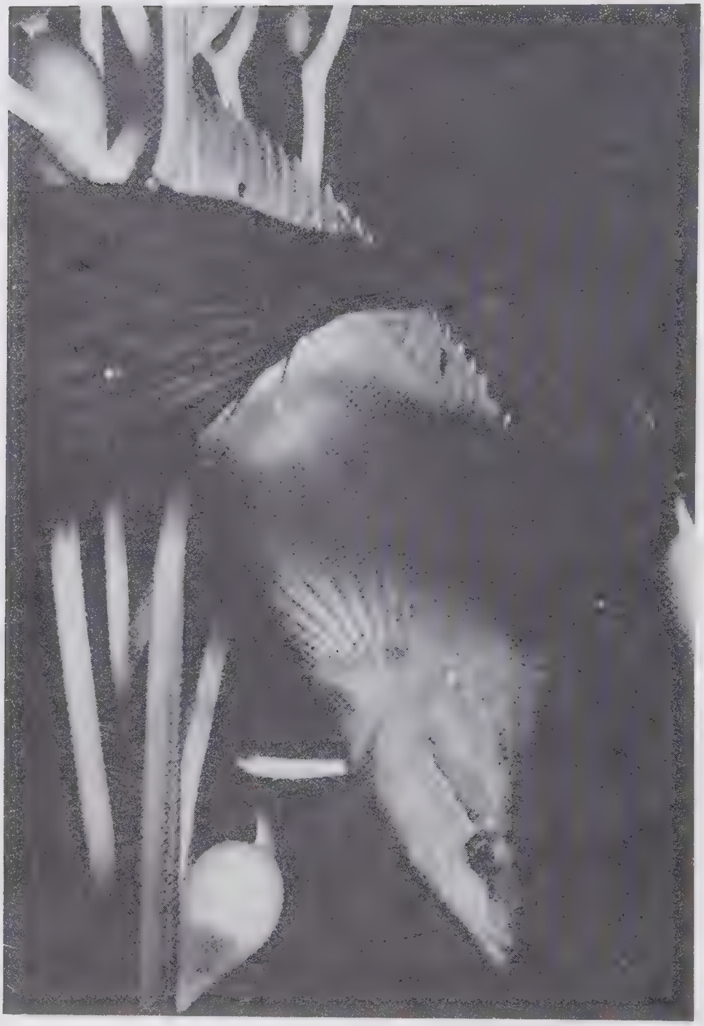

FIGURE 9.—While most of its smaller blennioid relatives go under cover at nightfall, the large clinid *Heterostichus rostratus*, here amid rising kelp stipes at night, shows a similar attitude at all hours, even though it seems to feed primarily by day.

was empty, and the two (163 and 207 mm) collected at midnight contained only well digested fragments. In comparison, among eight individuals (234-385 mm SL, $\bar{x}$ = 280) collected during midafternoon, four contained fresh food, one contained only well digested fragments, and three were empty.

Gobiidae: *Coryphopterus nicholsi*

Large numbers of the blackeye goby rested in exposed positions on sand bottoms in and around rocks throughout the day, when intermittently, they darted forward, or a short distance into the water column, and snapped at tiny prey. Few, however, were visible at night. Presumably most sheltered in the reef after dark—a pattern reportedly followed by four species of *Coryphopterus* in the tropical Atlantic Ocean (Smith and Tyler 1972). Gut contents indicate this species feeds little, if at all, after dark. Among the few individuals seen at night, seven (43-83 mm SL, $\bar{x}$ = 59.3) were collected during the hour before the first morning light; the gut of one was empty, and the other six contained only well digested items. In comparison, all 69 specimens (36-90 mm SL, $\bar{x}$ = 64.1) collected during the afternoon had food in their guts, with 61 of these (88%) containing recently ingested material.

Fishes That Feed Primarily at Night

The fishes that feed primarily at night clearly are specialized to detect and capture prey in the dark; nevertheless, under appropriate circumstances some also take prey during the day. The predominantly nocturnal species considered in this paper, with certain of their visual characteristics, are listed in Table 2. The following accounts of diel activities highlights major features of their crepuscular and nocturnal habits.

TABLE 2.—Some southern Californian fishes that feed primarily at night, with the spectral absorbance maximum (λ_{max}) of pigments extracted from their retinae.

Family and species	λ_{max} ± 95% C.I.	*N*	Other pigments[1]
Scorpaenidae:			
Scorpaena guttata[2]	496.7	2	0
Sebastes atrovirens	497.5	2	+
S. serranoides (subadult)	501.3	2	+
S. serriceps	496.4±1.0	3	0
Haemulidae:			
Xenistius californiensis	501.8±0.4	2	T
Sciaenidae:			
Seriphus politus[2]	502.2±1.5	3	0
Umbrina roncador	503.1±0.4	3	0
Embiotocidae:			
Hyperprosopon argenteum[2]	505.1±0.9	7	0
Mean	501.0		
Range	496.4-505.1		

[1] See Table 1. footnote 1.
[2] See Table 1, footnote 2.

Scorpaenidae: *Scorpaena guttata*

The sculpin rests immobile among rocks during the day (Figure 10) and generally is difficult to discern owing to its cryptic features. Although Limbaugh (1955) noted *S. guttata* on open sandy bottoms in deeper (to 60 m) water during the day, at our study sites it generally occurred among rocks. This fish seems well suited by its cryptic and immobile attitude to ambush prey that have come

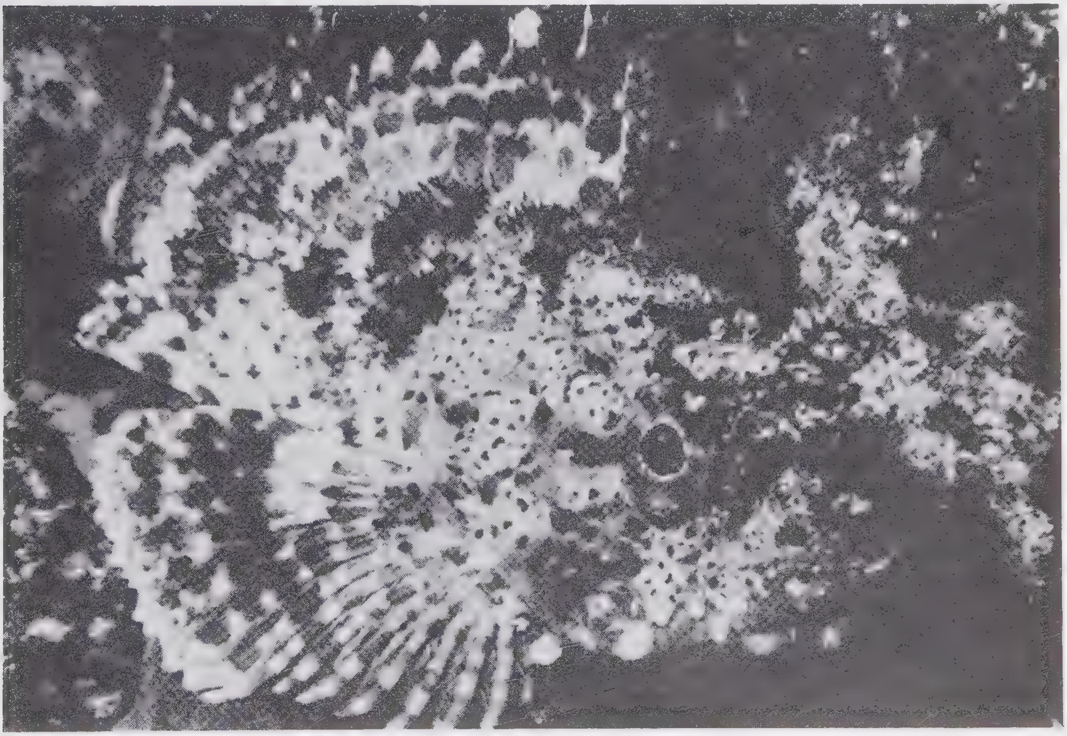

FIGURE 10.—The morphology, coloration, and sedentary behavior of *Scorpaena guttata* render it virtually invisible on the seafloor. Although many tropical scorpaenids use these features to advantage in ambushing prey during the day, *S. guttata* is primarily nocturnal.

within range of a short, explosive rush—a tactic used during the day by the Hawaiian scorpaenid, *Scorpaenopsis cacopsis*, which is similarly cryptic (Hobson 1974). Based on gut contents, however, *Scorpaena guttata* seems to capture most of its prey at night. All seven specimens (140-270 mm SL, $\bar{x}$ = 213) collected during the hour before dawn contained prey, many of them fresh. Major items were the crab *Podochelia* sp. (7 mm), the shrimps *Lysmata californica* (50 mm) and *Spirontocaris* sp. (15 mm), and the squid *Loligo opalescens* (120-190 mm), a species that was spawning in the area at the time. One *Scorpaena guttata* had captured a 108 mm *Chromis punctipinnis*, a species that shelters among the rocks at night (see above). In comparison, of seven individuals (164-237 mm SL, $\bar{x}$ = 208.3) collected among the rocks during midafternoon, the stomachs of four were empty, two contained only well digested octopuses, and one contained recently ingested prey (a crab, *Paraxanthias taylori*, 17 mm wide, and a shrimp, *Alpheus clamator*, 20 mm long). Crabs, shrimps, octopuses, squids, and fishes are recognized prey of this species (Limbaugh 1955; Quast 1968).

Scorpaenidae: *Sebastes atrovirens*

The kelp rockfish feeds at night while hovering solitarily in the water column close among the giant kelp plants (Figure 11). It is relatively inactive by day—often at rest on rocky substrata or hanging motionless close beneath the kelp canopy. This was the conclusion of Hobson and Chess (1976), who presented details of its diel feeding habits. Of 23 individuals (89-225 mm SL, $\bar{x}$ = 177.5) collected at night, more than 4 h after sunset, 20 (87%) contained prey, many recently ingested. Major prey were mysids (*Siriella pacifica*, 4-10 mm, and *Acanthomysis sculpta*, 4-10 mm), carideans (*Hippolyte clarki*, 7-14 mm, and *Eualus herdmani*, 5-10 mm), a gammarid (*Batea transversa*, 3-4 mm), and an isopod (*Paracercies crodata*, 2-9 mm).

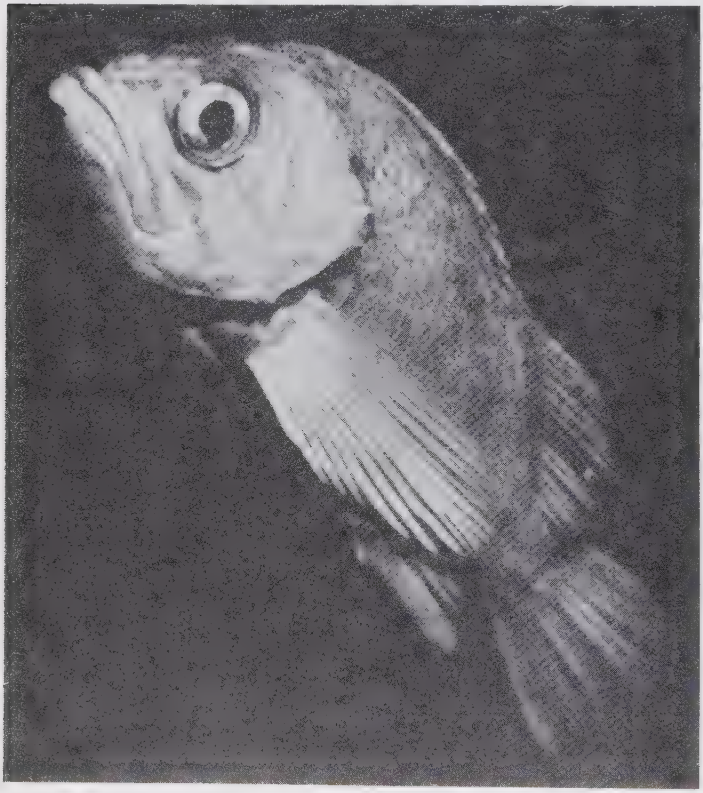

FIGURE 11.—In hovering tail-down close beneath the canopy of a kelp forest, this *Sebastes atrovirens* illustrates an attitude typical of many nocturnal predators that hunt in the water column. From this position they may use the relatively light water's surface as a contrasting background against which prey are visible.

Scorpaenidae: *Sebastes serranoides*

The olive rockfish progresses through stages characterized by distinctive trophic relationships (as described by Hobson and Chess 1976). These stages parallel those described above for the serranid *Paralabrax clathratus*, although the nocturnal element in the subadults is much stronger in *S. serranoides*.

Juveniles appear inshore when they are about 30 mm SL, and feed by day on zooplankton until they have grown to about 55-65 mm. When about 55 mm SL they begin to feed at night, a transition most of them complete by the time they are 65 mm SL. These nocturnal feeders, which are our major concern here, have assumed a pattern of activity that will characterize them until they are about 120-150 mm SL. By day they hover in relatively inactive schools, often at the edge of kelp forests, and during evening twilight they disperse over the surrounding area, where they forage in the water column. Many of them move away from the sheltering kelp to hover solitarily in open water. On the five evenings that the event was noted, the first one seen in a nocturnal mode away from cover was noted 16-30, $\bar{x}$ = 25.8, min after sunset. They remain in these positions throughout the night, often assuming a tail-down attitude, now and then darting a few centimeters forward and snapping at objects in the dark water.

When these fish shift to nocturnal foraging they also change their diet. From the copepods and other small zooplankton (about 1-2 mm long) they had taken during their earlier diurnal phase, they now capture larger organisms that swim in the nearshore water column only after dark (Hobson and Chess 1976). These nocturnal food habits were defined by study of gut contents. Of 72 individuals (65-157 mm SL, $\bar{x}$ = 85) collected more than 4 h after sunset, 70 (97%) were full of prey, many of them fresh. Major prey were the gammarid *Batea transversa* (2-5 mm), the mysid *Siriella pacifica* (3-9 mm), the cumacean *Cyclaspis nubila* (4-6 mm), the caprellid *Caprella pilidigita* (5-11 mm), and the isopod *Paracercies cordata* (3-6 mm).

Scorpaenidae: *Sebastes serriceps*

The treefish rests in rocky crevices at all hours of day and night, and evidence of specific feeding times is limited; nevertheless, it appears to be predominantly nocturnal or crepuscular. Of six individuals (138-227 mm SL, $\bar{x}$ = 189.5) collected during the hour before dawn, all contained relatively large crustaceans, including the shrimps *Lysmata californica* (12-70 mm), *Alpheus bellimanus* (60 mm), and *Spirontocaris* sp. (25 mm). Greatly reduced feeding during the day was evidenced by 22 individuals (122-330 mm SL, $\bar{x}$ = 276.1) collected during the afternoon from among rocks; of these, the guts of 13 (59%) were empty, and the other 9 contained material that was for the most part extensively digested—seven had each taken a single *Chromis punctipinnis* (68-135 mm SL), while other prey were the crab *Paraxanthias taylori* (16-38 mm wide), and the carideans *Lysmata californica* (38-45 mm) and *Herbstia parvifrons* (10 mm). Most of these prey had been in the guts for some time: only the two crabs appeared recently ingested. We suspect that all but the two crabs were captured during the previous night or morning twilight. We would expect the crustaceans to have been more accessible after dark, when we have seen the species in exposed locations. Further, the major prey in these collections, *C. punctipinnis*, generally swims high in the water column during the day, and would seem ill-suited then as prey of this bottom-dwelling rockfish. *Chromis punctipinnis* would be more vulnerable at night, when it settles to shelter on the seafloor (see account of *C. punctipinnis* above). However, the absence of *C. punctipinnis* in the guts of *Sebastes serriceps* taken before dawn indicates that the prey in these samples may have been captured during morning twilight, perhaps as they left cover for their ascent into the midwaters.

Haemulidae: *Xenistius californiensis*

The salema assembles in relatively inactive schools during the day, then disperses at nightfall and forages in the water column at night (Hobson and Chess 1976). This diel activity pattern is widespread among the many species of haemulids in tropical waters (Starck and Davis 1966, in the tropical Atlantic, and Hobson 1968a, in the Gulf of California). Frequently *X. californiensis* schools in the upper levels of the water column within the kelp forests, and during twilight, moves considerable distances to nocturnal feeding grounds. One location at Santa Catalina Island, known to be a nocturnal feeding ground for this species, was >400 m from the nearest point where the species had been seen during the day (Hobson and Chess 1976). On four evenings we noted when the first salema arrived on this feeding ground, and this proved to be between 34 and 40, $\bar{x}$ = 37.3, min after sunset. Once there, its behavior was much like that described above for nocturnally feeding olive rockfish. Its diet, too, proved similar to that of the rockfish. All 13 individuals (163-170 mm SL, $\bar{x}$ = 173.7) collected more than 3 h after sunset were full of food, much of it fresh. Prey were organisms that are in the nearshore water column only at night, with major forms being the gammarids *Batea transversa* (2-4 mm) and *Ampelisca cristata* (3-8 mm), the caprellid *Caprella pilidigita* (6-12 mm), the cumacean *Cyclaspis nubila* (2-4 mm), the mysid *Siriella pacifica* (4-10 mm), and epitokous nereid polychaetes (15 mm).

Sciaenidae: *Seriphus politus*

The queenfish schools in relatively inactive assemblages near shore during the day and disperses to feed in the water column at night after moving away from its daytime schooling sites (Hobson and Chess 1976). Thus, its diel activity pattern is similar to that of subadult *Sebastes serranoides* and *X. californiensis*, described above. The first *Seriphus politus* appeared at a nocturnal feeding site on four occasions at 38-60, $\bar{x}$ = 44, min after sunset. Food and feeding behavior of *S. politus* also are similar to the other two species. All 31 individuals (114-193 mm SL, $\bar{x}$ = 151) sampled later than 3 h after sunset contained prey, much of it fresh. All were larger zooplankton that are in the water column only at night, with major forms being mysids (*Siriella pacifica*, 3-11 mm, and *Acanthomysis sculpta*, 6-11 mm), a gammarid (*Batea transversa*, 2-4 mm), and an isopod (*Paracercies* sp., 2-7 mm).

Sciaenidae: *Umbrina roncador*

The yellowfin croaker schools close to sandy beaches during the day, and at nightfall disperses here and also to the regions immediately offshore. It feeds on organisms in the sediment, often probing with its snout to make the capture. Most of its foraging seems to occur at night. Of 20 individuals (191-255 mm SL, $\bar{x}$ = 210.8) collected more than 3 h after sunset, all but 1 contained prey, much of it fresh. Major items were sand-dwelling polychaetes, many of them tubicolous, with *Onuphis* sp. (15-40 mm) and *Nothria stigmaeus* (10-20 mm) predominating; other important prey were sand-dwelling gammarids, especially *Ampelisca cristata* (2-12 mm), *Acuminodeutopus heteruropus* (2-3 mm), and *Paraphoxus heterocuspidatus* (2-3 mm). Only limited feeding occurs by day, as attested by eight individuals (210-239 mm SL, $\bar{x}$ = 222.5) collected during the afternoon. Of these, only two contained fresh material (sand-dwelling amphipods, most of them *Ampelisca cristata*). These same two, and two others, also contained extensively digested polychaetes that obviously had been in the guts for some time; the other four (50% of the sample) were empty.

Embiotocidae: *Hyperprosopon argenteum*

The walleye surfperch is the only predominantly nocturnal species among the five embiotocids considered in this paper. It schools inactively by day, often close to shore, then disperses at nightfall and moves to feeding grounds some distance away (Hobson and Chess 1976; Ebeling and Bray 1976). It forages in the water column, where it takes the larger zooplankton that are numerous there only after dark. Thus, *H. argenteum* has habits similar to those of the other nocturnal planktivores described above. Although it usually forages lower in the water column than these others, its diet and feeding behavior also are similar: of 29 individuals (100-157 mm SL, $\bar{x}$ = 126) collected over nocturnal feeding grounds at night, or from recently formed schools before sunrise, 28 (97%) contained food, much of it fresh. Major prey items were the gammarids *Batea transversa* (2-4 mm), *Ampelisca cristata* (3-4 mm), and *Ampithoe* sp. (4-6 mm); the cumacean *Cyclaspis nubila* (2-4 mm); the isopod *Paracercies* sp. (2-5 mm); and the caprellid *Caprella pilidigita* (4-10 mm).

Fishes That Feed Day and Night

Only two of the species studied resist classification as being either primarily diurnal or primarily nocturnal in their feeding activities. Both seem equipped to exploit circumstances that permit effective feeding during all hours of day and night. They are listed in Table 3, along with certain of their visual characteristics. The following accounts of their diel foraging activities puts their diurnal and nocturnal habits in perspective.

Cottidae: *Leiocottus hirundo*

The lavender sculpin rests immobile in exposed locations on sandy substrata, usually near rocks and algae, at all hours of day and night. On the

TABLE 3.—Some southern Californian fishes that feed day and night, with the spectral absorbance maximum (λ_{max}) of pigments extracted from their retinae.

Family and species	λ_{max} ±95% C.I.	*N*	Other pigments[1]
Cottidae:			
Leiocottus hirundo	500.0	2	0
Pleuronectidae:			
Pleuronichthys coenosus	500.9±0.5	3	T
Mean	500.5		

[1] See Table 1, footnote 1.

rare occasions that feeding was observed, this fish moved only a few centimeters to snatch an object in the sand. Eight specimens (130-196 mm SL, $\bar{x}$ = 177) were collected from a variety of habitats during the afternoon. Six (75%) contained food in their stomachs, with the predominant prey being the polychaetes *Glycera capitata* (30-85 mm), *Lumberineris* sp. (20-90 mm), and terrebellid tentacles. One had taken the gammarid *Ampelisca cristata* (12 mm), and one a holothurian (17 mm). Comparable data on nocturnal feeding was obtained from eight specimens (66-194 mm SL, $\bar{x}$ = 136) collected during the hour before dawn. Again, six (75%) contained food in their stomachs, with polychaetes—*Glycera* sp. (35 mm), *Nothria stigmatis* (8 mm), and a terrebellid (30 mm)—the major prey, though less so than during the day. Gammarids, especially *Ampelisca cristata* (2-6 mm) were important to these nocturnal individuals, as was the clam *Solemya valvus* (8-10 mm). But these differences in prey selection between day and night may relate to fish size rather than to time of feeding: two *Leiocottus hirundo* collected during the night were smaller (66 and 84 mm) than any taken by day, and it was these that had preyed mostly on gammarids. Aside from these minor differences in food composition, feeding habits appear similar day and night: stomachs of the day feeders averaged 75% full, and contained $\bar{x}$ = 4.2 items, compared with an average of 69% full and $\bar{x}$ = 4.8 items for the night feeders.

Pleuronectidae: *Pleuronichthys coenosus*

The C-O turbot rests immobile on sandy substrata at all hours of day and night—usually exposed but sometimes under a thin layer of sediment. Often it occurs in the same habitat as *L. hirundo*, but more so than the cottid it ranges into regions of open sand, where its highly variable coloration often matches the surroundings. We have observed feeding only in daylight, when typically this species rests motionless, with body somewhat elevated on dorsal and anal fins and head poised above the substratum (Figure 12). Its mobile, closely set eyes are oriented vertically on a bony ridge, and function almost as if set in a turret. This arrangement permits the fish to scan the seafloor close at hand, probably for moving sediments or other signs of prey that are just below the surface. Occasionally we have seen individuals that had been immobile in one spot for some time move a meter or so across the seafloor, pause for a moment, and then drive their heads into the sediment. Usually we were unable to see what they had taken, but daytime quarry were identified in the 11 specimens that contained food out of 14 (161-212 mm SL, $\bar{x}$ = 186) collected from sandy substrata during the afternoon (stomachs averaged 47% full). The major prey were polychaetes, especially terrebellid tentacles. Although we did not observe feeding at night, prey were identified in all 11 specimens (159-220 mm SL, $\bar{x}$ = 183.5) collected during the hour before dawn (stomachs averaged 72% full). Again, polychaetes, especially terrebellid tentacles, predominated. Clearly its trophic relationships are similar to those of *L. hirundo*, except that it may be more able to feed at night.

DISCUSSION

Events during twilight and at night in Californian marine habitats can be compared with equivalents on tropical reefs. Tropical activity patterns have been described (Hobson 1965, 1968a, 1972, 1974; Starck and Davis 1966; Collette and Talbot 1972; Smith and Tyler 1972; Vivien 1973), as has scotopic vision in tropical fishes (Munz and McFarland 1973). Below we relate our findings with Californian coastal fishes to these and other studies made elsewhere. First we consider crepuscular and nocturnal activity patterns and then scotopic spectral sensitivity, first in relation to ambient light, and then to bioluminescence.

Activity Patterns

In relating diel activity patterns of fishes in Californian waters near Santa Barbara to fishes on tropical reefs, Ebeling and Bray (1976) referred to the Californian species as "kelp-bed" fishes. We assume they implied a broad concept of this term that includes fishes sometimes in kelp forests, but more characteristic of other habitats. This is because the tropical side of their comparison (which

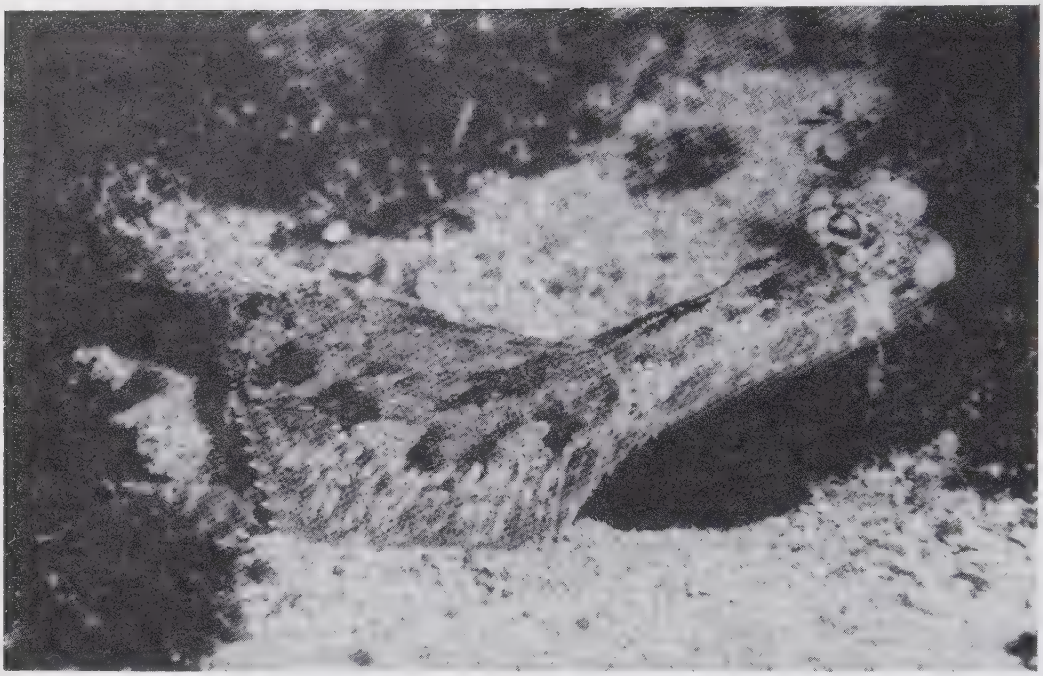

FIGURE 12.—*Pleuronichthys coenosus*, which feeds day and night, largely on sand-dwelling polychaetes, has eyes on either side of a bony ridge set almost as if in a turret. This arrangement increases its ability to scan the surrounding seafloor for prey and threatening predators.

is based on observations by Hobson 1965, 1968a, 1974; Starck and Davis 1966; and others) involves species (often referred to as coral-reef fishes) from a variety of contiguous habitats. A comparison of diurnal and nocturnal behavior requires a multihabitat view because so many fishes move from one habitat to another between day and night.

The general scene in Californian nearshore habitats differs dramatically between day and night. A major aspect of this difference is the sharp drop in observed activity among fishes on reefs after dark. Describing an "aura of desolation..." in the "notably lackluster night life,..." Ebeling and Bray (1976) considered this feature of kelp forests to be in contrast to tropical reefs. But on tropical reefs, too, one notes less activity at night than during the day (e.g., Starck and Schroeder 1965). Nevertheless, there may be an especially pronounced difference where Ebeling and Bray studied, because the relative dearth of nocturnal activities there led them to conclude: "...in kelp beds there is no broad replacement for the 'day shift' of fishes at night." In particular, they reported an absence of fishes that move from daytime assemblages on reefs to nocturnal feeding grounds on adjacent sand, and also to there being relatively few nocturnal planktivores. But the situation they described is unlike that which prevails in the more southerly waters around Santa Catalina, where many species are most active at night. Following a pattern widespread in the tropics, for example, *Xenistius californiensis*, *Umbrina roncador*, *Seriphus politus*, and *Hyperprosopon argenteum* (to mention species considered in this report) are relatively inactive in schools near shore, reefs, or kelp forests by day, and disperse over feeding grounds elsewhere at night. It may be significant, however, that with the exception of *H. argenteum*, these are species with close tropical affinities (Table 4). In contrasting the relative absence of nocturnal planktivores at their Santa Barbara study site, with the many such forms at Santa Catalina (as reported by Hobson and Chess 1976), Ebeling and Bray suggested

TABLE 4.—Geographic affinities[1] of the fishes studied.

I. Warm-temperate representatives of basically tropical families or genera; species that do not range into the colder waters northward from central California. Twelve species:

Scorpaena guttata
Paralabrax clathratus
Xenistius californiensis
Seriphus politus
Umbrina roncador
Medialuna californiensis
Girella nigricans
Chromis punctipinnis
Hypsypops rubicunda
Halichoeres semicinctus
Oxyjulis californica
Semicossyphus pulcher

II. Temperate representatives of basically tropical families; species that range widely into the colder waters northward from central California. Two species:

Atherinops affinis
Coryphopterus nicholsi

III. Warm-temperate representatives of temperate families or genera; species that do not range northward from central California. Five species:

Sebastes atrovirens
S. serriceps
Leiocottus hirundo
Alloclinus holderi
Gibbonsia elegans

IV. Representatives of temperate families or genera; species that range widely northward from central California. Eight species:

Sebastes serranoides
Brachyistius frenatus
Cymatogaster aggregata
Damalichthys vacca
Embiotoca jacksoni
Hyperprosopon argenteum
Heterostichus rostratus
Pleuronichthys coenosus

[1]Based on ranges given in Miller and Lea (1972)

that the difference may reflect the proximity of Santa Barbara to Point Conception, the northern boundary of the warm-temperate zoogeographic region (Hubbs 1960; Quast 1968; Briggs 1974).

Certainly there is a strong tropical influence in many of the more clearly defined crepuscular and nocturnal activity patterns among southern Californian fishes. Species with the most distinctive patterns tend to be warm-temperate representatives of what basically are tropical families. The three Californian labrids, for example, seek and leave nocturnal shelter at precise times relative to sunset and sunrise, just as their tropical relatives do. And the two Californian pomacentrids shelter under reef cover at night in the same manner as tropical pomacentrids. Similarly, of the species listed above that school inactively by day and disperse to feed at night, most represent the predominantly tropical families Haemulidae and Sciaenidae. Clearly these behavior patterns are rooted deeply in their tropical ancestry, and are as characteristic of their kind as the more generally recognized morphological features that define their families. Ebeling and Bray recognized the strong influence that ancestral relationships exert on activity patterns, and distinguished "temperate derivatives" from "tropical derivatives." (Unaccountably, however, they considered *Paralabrax clathratus* and *Coryphopterus nicholsi* to be of temperate stock, even though the affinities of both are predominantly tropical.) These relationships, then, are insightful in understanding how activity patterns are integrated in southern Californian nearshore fish communities. The geographical affinities of the various species (Table 4) are helpful in gaining an overview of these relationships.

Because nearshore communities in warm-temperate southern California mix fishes of temperate and tropical affinities, it is tempting to interpret behaviors in terms of interactions between these two lineages. Such comparisons are risky. For example, Ebeling and Bray (1976) stated: "It is paradoxical that the 'tropical derivatives'...persist in their complex...shelter-seeking while many primarily temperate fishes remain exposed." We see no paradox here. On tropical reefs, too, many diurnal fishes remain exposed at night, while others seek cover. Size often influences which strategy is used. For example, while smaller acanthurids (surgeonfishes) and chaetodontids (butterflyfishes) generally are sheltered, larger members of their families often rest exposed (Hobson 1972, 1974). Ebeling and Bray went on to suggest: "... the 'tropical derivatives' may...compete more successfully against primarily temperate species such as surfperches for shelter on the reef." This speculation, too, is unsupported by our observations. Most of the temperate species involved here are widespread northward (see Table 4, Group IV), well beyond the ranges of the tropical derivatives, and there too they are exposed at night (E. S. Hobson pers. obs.).

We doubt that nocturnal shelter sites are in short supply on California reefs except under exceptional circumstances. The places we identified as resting sites of *Semicossyphus pulcher* were just sporadically occupied, which seems an unlikely circumstance if there is strong competition for these sites. But clearly there is a shortage of shelter sites where the diurnal planktivore *Chromis punctipinnis* is so numerous that at night resting individuals overflow from the rocks and actually pile up on the adjacent sand. Apparently this exceptional situation exists where the zooplankters on which this fish feeds are abundant by day, but appropriate nocturnal shelter is limited. Significantly, however, the competition for this shelter appears to be intraspecific.

A casual appraisal of southern Californian fishes agrees with Ebeling and Bray (1976) that activities among fishes of the kelp-bed community are "... more loosely 'programmed'" than among fishes in tropical reef communities. A similar condition has been described for temperate lake fishes

(Helfman 1979). This position is strengthened by the more clearly defined behavior in the Californian representatives of tropical families. But at least two considerations complicate this comparison. First, activity patterns, no matter how highly structured, will be less evident in temperate fish communities because a greater proportion of the species there are sedentary. As stated for tropical fishes (Hobson 1972), relative activity in sedentary species is difficult to quantify. Second, and perhaps more important, because there are far fewer species in the temperate habitats, community activity patterns will be less distinct if only because they are defined by fewer forms. It need not follow that activities of each species are less structured. Despite these cautions, however, it is generally accepted that organisms tend to have less specialized habits where species are fewer, and this circumstance should produce more loosely structured activities.

Whether or not activities of individual species are less structured in California than in the tropics, certainly the overall community patterns in California are less clearly defined. In examining the changeovers between diurnal and nocturnal modes, for example, we found little evidence of the detailed community transition-patterns that typically characterize these phenomena on tropical reefs (Hobson 1972; Collette and Talbot 1972; Domm and Domm 1973; McFarland et al. 1979). In particular, we were unable to clearly define a "quiet period," that 15-20 min segment of twilight on many tropical reefs when smaller fishes—both diurnal and nocturnal—have vacated the water column. Based on studies in the tropics (Hobson 1968a, 1972; Munz and McFarland 1973), the quiet periods are considered times of increased danger from predators when smaller fishes find it adaptive to avoid exposed positions. So if the quiet periods are less evident in California, it could indicate reduced crepuscular predation there.

When the sequence of twilight events identified at Santa Catalina Island is related to the timing of the quiet period at Kona, Hawaii (Figure 13), there might appear to be more overlap between the diurnal and nocturnal modes in California. For instance, as the nocturnal juveniles of *Sebastes serranoides* move into exposed locations (Figure 13, event 5), they sometimes pass above active labrids (Figure 13, events 2, 3, and 4) and close to the

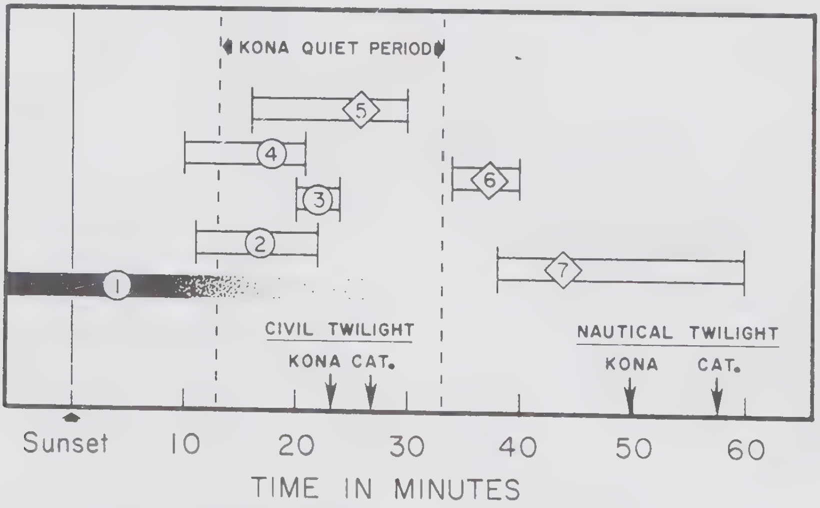

FIGURE 13.—Events during the evening changeover between day and night at one southern Californian site from August to November 1973, relative to timing of the quiet period at Kona, Hawaii (Hobson 1972). (The Californian site is illustrated in Hobson and Chess 1976: fig. 2, 3.) Circles represent diurnal species, diamonds represent nocturnal species. Event 1 is based on estimates, events 2-7 on counts, with bars encompassing range, and numbers located at mean. 1. Migration of *Chromis punctipinnis* to nocturnal resting area: progressive disintegration of bar represents decreasing numbers of individuals in migrating groups ($n = 6$). 2. Time last *Oxyjulis californica* was seen active ($n = 4$). 3. Time last *Halichoeres semicinctus* was seen active ($n = 6$). 4. Time last *Semicossyphus pulcher* departed observation site for nocturnal resting places elsewhere ($n = 4$). 5. Time first *Sebastes serranoides* appeared at open water feeding ground ($n = 5$). 6. Time first *Xenistius californiensis* arrived on feeding ground ($n = 4$). 7. Time first *Seriphus politus* arrived on feeding ground ($n = 4$). Times of civil and nautical twilight are from Nautical Almanac (U.S. Naval Observatory, Washington, D.C.) and are means of times on dates observations were made.

last migrating *Chromis punctipinnis* (Figure 13, event 1). But this apparent overlap can be explained without evoking a more relaxed regime. Although the three species of Californian labrids retire relatively late (even considering the longer twilight at temperate latitudes), they grow larger than most of their tropical relatives, and it is generally true that among diurnal fishes larger individuals retire later (Hobson 1972). Similarly, there are tropical equivalents to the relatively early shift made by juvenile *S. serranoides* to its nocturnal mode. In the western tropical Pacific Ocean, for example, the largely transparent nocturnal juveniles of some apogonids move away from shelter long before their larger adults. Some of them — many < 30 mm long — move out as early as 10 min after sunset (E. S. Hobson unpubl. obs.). This entry into exposed locations at a time when many piscivorous predators hunt most effectively might seem in conflict with the quiet-period concept. But in the dim twilight we are not surprised that these inconspicuous little fishes seem to go unseen by the visual hunters that so seriously threaten the more visible adults. Certainly these juveniles go unseen by human eyes at this time, except upon close inspection with a diving light, and so fail to detract from the aura of inactivity that characterizes the quiet period.

So what might appear to be a more loosely structured sequence of events during twilight in California may instead reflect the lesser number of species that define the transition pattern there. At least some semblance of a quiet period is evident. On the occasions depicted in Figure 13, the numbers of migrating *C. punctipinnis* declined sharply about 10 min before the juvenile *S. serranoides* first appeared, and after that only scattered small groups passed that way. Considering the tremendous numbers of *C. punctipinnis* in that area (we have never seen a single species so dominant on coral reefs), numerous exceptions from the norm should be expected. Furthermore, major species that occupy the water column at night — *Xenistius californiensis* and *Seriphus politus* — did not arrive until about 20 min after the vast majority of *C. punctipinnis* had passed through. So although crisp definition is lacking, there is evidence of a quiet period in Californian waters from about 15 to 35 min after sunset.

It remains uncertain whether the dangers smaller fishes face during twilight in southern Californian coastal waters are as intense as those faced on tropical reefs. Limited data from gut contents indicate that such major predators as *Paralabrax clathratus* and *Sebastes serriceps* are primarily crepuscular when capturing smaller fishes. Unfortunately, we can no longer directly observe much of the predation that has influenced the evolution of coastal fishes in southern California. This is because during recent decades populations of the larger predators involved — including the giant seabass, *Stereolepis gigas*, and the white seabass, *Cynoscion nobilis* — have been decimated by fishermen. Nevertheless, as we discuss next, the possibility that Californian fishes have faced intensified selection pressures during twilight is also indicated by the nature of their scotopic visual pigments. Significantly, despite the varied forms and habits of these fishes, the maximum absorptions (λ_{max}) of their scotopic pigments cluster about 500 nm, which indicates strong selection for enhanced photosensitivity over this segment of the spectrum.

Scotopic Spectral Sensitivity and Ambient Light

Tropical reef fishes have scotopic pigments that cluster about wavelengths that spectrally match twilight, which underwater is bluer than the light of day or night (Munz and McFarland 1973). In developing their Twilight Hypothesis, Munz and McFarland pointed out that because dawn and dusk are the most dangerous times for fishes on tropical reefs (Hobson 1972), even slightly increased photosensitivity during twilight may be crucial.

The Twilight Hypothesis is a variation of the Sensitivity Hypothesis (Lythgoe 1966), which declares that visual sensitivity is improved when absorption of photo pigments matches ambient light. The scotopic pigments of both aquatic and terrestrial vertebrates are known to cluster about narrow wave bands, but at different regions of the spectrum (for review, see McFarland and Munz 1975b). Among fishes, the scotopic pigments broadly match the spectral transmission of the water in which the fishes live (Lythgoe 1972). Deep sea fishes, for example, have scotopic pigments that tend to be even more blue sensitive (λ_{max} from 478 to 490 nm: Denton and Warren 1956; Munz 1957), than tropical marine fishes (λ_{max} from 489 to 500 nm: Munz and McFarland 1973), and the pigments of freshwater fishes are green sensitive (λ_{max} from 503 to 540 nm: McFarland and Munz

1975b). The present study shows that fishes associated with Californian kelp forests have pigments that are most sensitive to blue-green light (λ_{max} from 496 to 506 nm).

If the adaptive advantage of matching ambient light lies in heightened photosensitivity, then the match should be to light that prevails when selection for improved vision is most intense. We are not surprised, therefore, that the λ_{max} values for fishes in a given habitat match not the light of day or night, but rather the bluer twilight, and thus the fishes are equipped to meet an intensified threat from crepuscular predators. In clear tropical waters, for example, the λ_{max} values of the scotopic pigments in reef fishes cluster about 492 nm, which in that habitat matches twilight, rather than the greener light of day or night (Munz and McFarland 1977). Of course, the spectral position of this match is influenced by the light transmission characteristics of water in that particular habitat. For example, in most fresh waters the match is made above 520 nm, but this position nevertheless approximates the λP_{50} of twilight in these very green waters and is in fact toward the blue from light that prevails there during day and night (McFarland and Munz 1975c).

As could have been predicted from the Sensitivity Hypothesis, the scotopic pigments of fishes in the blue-green coastal water of California cluster at wavelengths intermediate between those of fishes on coral reefs and those of fishes in freshwater, at about 500 nm (Tables 1-3). The match with twilight, however, is less clear in Californian waters than in the other two environments because, we believe, photic conditions in Californian waters are more variable. Nevertheless, the tight clustering of scotopic pigments around 500 nm in the Californian fishes better matches ambient light during twilight than at night. Both moonlight and starlight are richer in red light than daylight or twilight (Munz and McFarland 1977), and for all water conditions we encountered at Santa Catalina Island downwelling light at night would have λP_{50} values well above 520 nm (Figure 5). Only during twilight does ambient light underwater shift far enough toward the blue-green region of the spectrum (Figures 3, 4) to produce a close match with the visual pigment λ_{max}.

In evaluating the impact of crepuscular predators on the spectral position of scotopic pigments, however, we must not forget that other selection pressures are operating. We would expect scotopic pigments in fishes to be particularly responsive to such alternate pressures at night, which is especially "short of light" (Dartnell 1975). Certainly fishes must be sensitive to the emissions of bioluminescent organisms, because few visual cues could be more apparent than a flash of light in the dark.

Scotopic Spectral Sensitivity and Bioluminescence

Bioluminescence often signifies underwater movement. According to Hobson (1966), "In many areas of the sea at night, a moving object is readily observed due to the luminescence of many minute planktonic organisms, mostly protozoans, which light up when disturbed. These organisms are often so numerous that while making observations underwater I have been able to identify, to species, fishes that swam actively among them. This was not because the fish itself was illuminated, but rather because there were so many minute luminescent organisms about the fish that its form was essentially traced out in tiny flecks of light." If such cues are evident to human eyes, adapted to a diurnal, terrestrial existence, the capacity to sense and to orient by them must be highly refined in animals like fishes that have evolved in this environment.

Bioluminescence offers an especially effective way to detect predators or prey because predator-prey interactions generally involve movement, and luminescence by plankton is greatly increased in the turbulent water around moving objects. We believe, as did Burkenroad (1943), that this fact has had enormous impact on the nocturnal tactics of both predators and prey. The motionless attitude that characterizes nocturnal planktivorous fishes when they hunt probably is enforced by the need to minimize turbulence in the water about them. By minimizing turbulence they minimize the firing of luminescent organisms that would betray their presence, and so hover unseen in the dark, ready to strike when nearby prey advertise their positions by disturbing the plankton. This tactic is in essence an ambush and probably is effective only at short range. Reasons for this limitation are two. First, an attack, once launched, is immediately identified by flashing plankton, thus giving prey more than a short distance away time for evasive maneuvers. Second, a long-range attack directed at plankton luminescing around a particular prey may be led to the prey's wake, because the targets that elicited the attack are left behind when the prey darts away. Probably predators can be led by luminescent plankton to prey over some distance (Nichol 1962), but we suggest the approach must be made with great stealth to avoid turbulence and resulting luminescence. Surely such limitations preclude many kinds of predatory activities after dark, especially when the prey are as agile as most small fishes. In fact, the diminished threat from predators that smaller reef fishes enjoy at night (Hobson 1973, 1975, 1979) may stem largely from the difficulties predators have at this time moving undetected to within striking range.

If fishes use luminescent plankton to detect predators and prey, undoubtedly they have experienced strong selection pressures to enhance this detection. An obvious adaptive response to such pressures would be a match of the scotopic visual pigments to the emission spectra of the luminescent plankton. Certain vertebrates living at great depths, or in the open ocean, reportedly have scotopic pigments that match the luminescent emissions of organisms with which they interact, socially or as predator or prey (Clarke 1936; Munz 1958a; Lythgoe and Dartnall 1970; McFarland 1971; Locket 1977). These animals, however, interact directly with the luminescent organisms, whereas we stress indirect interactions. Of course, the principle is the same either way—detection is enhanced by matching visual pigment absorption to a luminescent emission.

The emission spectra of most luminescent plankton, as exemplified by *Noctiluca miliaris* and *Gonyaulax polyedra* (Figure 5), indicate that fishes would sense the emitted photons best with blue-sensitive visual pigments that have λ_{max} values near 490 nm. But this holds only before the light has passed through water. As noted above, the spectrum of light changes as it travels through water, with the degree of change sharply affected by the water's clarity. Clearly any such change will favor a different λ_{max} value in visual pigments.

The relative effectiveness of visual pigments with differing λ_{max} values in waters of differing clarities can be estimated with some simple calculations. Given the relative attenuation of light at each wavelength, which is a function of water type, we can compare the relative photoabsorption of different visual pigments at increasing distances from the luminescent source. Let us consider, for example, how a series of pigments with λ_{max} values at 10 nm intervals between 450 and 550 nm, each at 0.4 absorbance units, would absorb the light emitted by *Noctiluca* as this light passes through differing clarities of seawater, as defined by Jerlov (1968). The relative photoabsorption of each pigment at a given distance from the source can be estimated by multiplying that pigment's percentage absorption at each wavelength by the relative amount of light available at that wavelength and then integrating the products over all wavelengths (Figure 14). Thus, to see luminations from an organism like *N. miliaris* at a distance of 3 m in coastal waters (as at Santa Catalina), fishes would best have visual pigments with λ_{max} values between 500 and 510 nm. And as range increases, and water clarity decreases, photodetection of this luminant source would be improved by shifting the λ_{max} position slightly, but continuously, toward the greener wavelengths (Figure 15).

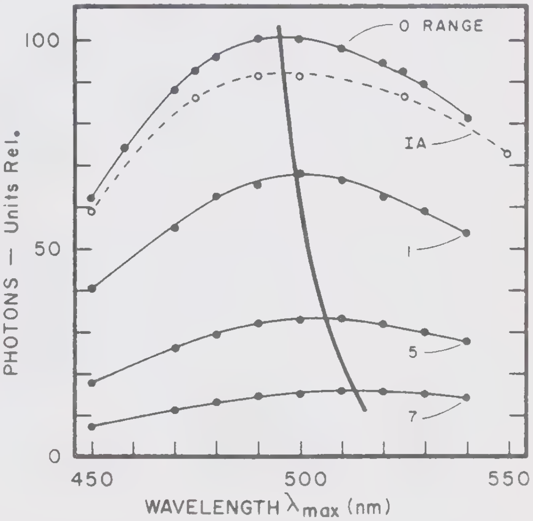

FIGURE 14.—Expected relative effectiveness of visual pigments with differing λ_{max} values (positioned at wavelengths indicated by circles) in sensing luminescent emissions of *Noctiluca miliaris* under varying circumstances. Top curve, for reference, represents effectiveness at zero range (no alteration of emission spectrum by intervening water); dashed curve (with open circles), for comparison, represents effectiveness at distance of 3 m in clear tropical water (water type 1A of Jerlov 1968); three lower curves represent relative effectiveness in waters of decreasing clarity (water types 1, 5, and 7 of Jerlov 1968). Vertical line crosses each curve at the optimal λ_{max} position. Method of calculation in text.

In reality, of course, the reduced visibility in turbid water sharply limits the practical extent of such a shift. During heavy phytoplankton blooms, for example, even large objects in full daylight are

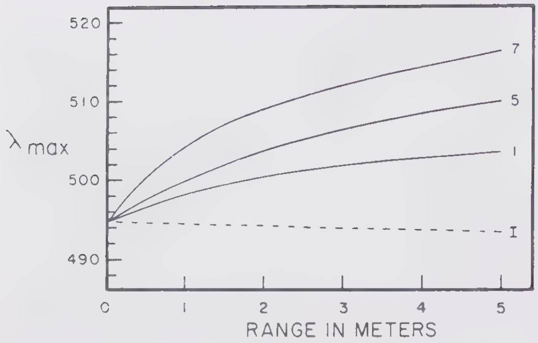

FIGURE 15.—Calculated optimum λ_{max} position for absorption of luminescent emissions of *Noctiluca miliaris* at increasing range in waters of differing clarity. Water types I, 1, 5, and 7 of Jerlov (1968). Solid lines = coastal waters of increasing turbidity; dashed line = clear tropical water.

invisible beyond 2-3 m. Obviously under such conditions bioluminescence, too, would be invisible at these distances. Probably most meaningful interactions involving fishes and the bioluminescent emissions of plankton occur over distances of just a few meters or less, and to see bioluminescence at these ranges in the waters of varying visibility that surround Santa Catalina fishes probably would best have visual pigments with λ_{max} values at a little above 500 nm (Figure 15).

One might expect diurnal fishes to be less sensitive than nocturnal or crepuscular fishes to selection pressures on scotopic pigments because they are less active under low light. But among species studied at Santa Catalina the λ_{max} values scarcely differ between the two groups (diurnal feeders: $\bar{x}$ = 499.1 nm, range = 496.1-505.8—Table 1; nocturnal feeders: $\bar{x}$ = 501 nm, range = 496.1-505.1—Table 2). Perhaps there is little difference here because many of these diurnal feeders are exposed at night and need means to detect threatening predators. In fact, if the fishes are grouped according to their relative exposure after dark, rather than by how active they are at this time, their λ_{max} values show a clear pattern (Table 5). Those fishes that are exposed at night, compared with those that are sheltered, tend to have scotopic pigments with spectral sensitivities closer to what we consider optimum for detecting bioluminescence in Californian coastal waters. This would mean that, despite their apparent quiescence, at least many diurnal fishes remain visually alert for potential threats during the night.

So the similar λ_{max} values in the diurnally feeding *Atherinops affinis* (505.8 nm) and the nocturnally feeding *Hyperprosopon argenteum* (505.1 nm) may answer the similar threats both face while exposed in the water column at night. We assume the increased sensitivity to bioluminescence would also benefit *H. argenteum* in feeding, but suspect this advantage would be less forceful. The need to evade predators should be sharper than the need to capture prey. Both needs are critical, but there is less tolerance for error on defense than on offense. A fish as prey is likely to be eliminated the first time it errs in responding defensively to an attack, but the same fish as an attacker may err many times without serious consequences.

Bioluminescence, triggered by movement, represents a well-defined indicator of immediate danger that can effectively focus selection pressures on a narrowly defined adaptive response. Moonlight and starlight would seem less suited for this because neither so effectively identifies specific threats and because the impact of both

TABLE 5.—Relative exposure at night, and λ_{max} position of scotopic visual pigments in certain southern Californian marine fishes.[1]

Relative exposure at night	Species		λ_{max} mean	λ_{max} range
I. Fully exposed in water column	*Atherinops affinis* *Sebastes serranoides* *Xenistius californiensis* *Seriphus politus*	*Brachyistius frenatus* *Cymatogaster aggregata* *Hyperprosopon argenteum*	502.1	500.4-505.8
II. Fully exposed on or near seafloor, often on open sand	*Umbrina roncador* *Damalichthys vacca* *Embiotoca jacksoni*	*Leiocottus hirundo* *Pleuronichthys coenosus*	501.1	500.0-503.1
III. Partially or fully sheltered by rocks or algae	*Scorpaena guttata* *Sebastes atrovirens*[2] *S. serriceps* *Paralabrax clathratus* *Girella nigricans* *Chromis punctipinnis*	*Hypsypops rubicunda* *Semicossyphus pulcher* *Alloclinus holderi* *Heterostichus rostratus* *Coryphopterus nicholsi*	497.3	496.1-499.7

[1] Of species studied, *Medialuna californiensis* is excluded because its nocturnal habits remain uncertain (see text), and *Halichoeres semicinctus* and *Oxyjulis californica* are excluded because they have a different type of visual pigment (see Table 1, footnote 3).

[2] Even though *S. atrovirens* feeds in the water column at night, these activities occur close to rising kelp stipes or just beneath the surface canopy

tends to be diffused over a greater range of visual circumstances. Bioluminescence is more constant: the spectral compositions of moonlight and starlight change with water depth and atmospheric conditions, but the spectral composition of bioluminescence is independent of these variables. And, of course, there is less light from moon or stars with increased water depth, which, again, is untrue of a bioluminescent emission. So it is not surprising that the narrow range of λ_{max} positions in visual pigments of Californian fishes more closely matches bioluminescence than it does moonlight or starlight (Figure 16).

Undoubtedly moonlight and starlight have strong influences on nocturnal relationships among predators and prey. But probably both help fishes more on offense than on defense. Predators can position themselves, and time their attacks, to play both types of light to their advantage, and to the prey's disadvantage. By charging at prey from below, for example, predators view their targets against the water's relatively light surface, while their own movements are masked by the surrounding gloom (Hobson 1966). Certainly attacks that so often spring from the shadows would greatly dilute a defensive advantage prey might gain with spectral sensitivities that match moonlight or starlight. Under these circumstances prey face a broad range of threats that calls for a more generalized response. So we can understand why many smaller reef fishes that habitually range into the water column at night stay closer to shelter under moonlight (Hobson 1968a).

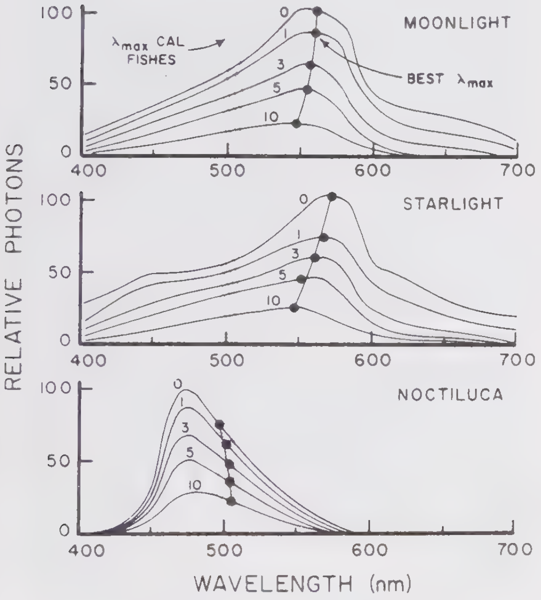

FIGURE 16.—Relationships between the spectral distributions of moonlight, starlight, and bioluminescence (as produced by *Noctiluca miliaris*) in seawater typical of southern California and the spectral sensitivities of fishes that live there. The five curves for each type of light represent the spectral distribution expected to reach a fish at the distance (in meters) indicated by the number that accompanies each curve. The curves depict moonlight and starlight off a flat reflector at a depth of 3 m (using values from Munz and McFarland 1977), and the luminescence of *N. miliaris* (using values from Nicol 1958), in water equivalent to typical conditions at Santa Catalina Island (Coastal Type 1 of Jerlov 1968). The solid circle on each spectral curve identifies the wavelength to best match with a visual pigment for maximum photosensitivity, and the stippled column represents the spectral range of maximum photosensitivity in scotopic pigments of Californian fishes (λ_{max}). Note that these coincide only with bioluminescence.

Despite the offensive advantage that certain predators likely gain from moonlight (or starlight), their scotopic visual pigments tend to be better matched to bioluminescence (or twilight), probably because this answers a more pressing need on defense. So it would seem that even those species that have special tactics to use moonlight or starlight to better see their prey must compromise with visual pigments less than optimal for this task. Included are those nocturnal planktivores, like subadult *Sebastes serranoides*, that characteristically hover tail-down in the water column, where apparently prey are visible to them against moonlight or starlight from above. Included, too, are those predominantly diurnal fishes, like *Paralabrax clathratus* and *Cymatogaster aggregata*, that apparently are able to hunt at night close to sand where light levels are elevated by reflected moonlight and starlight. We suggest not that their visual pigments are unsuited to see prey by moonlight or starlight, but rather that these pigments simply could have better spectral sensitivities for this particular job (Figure 16).

These arguments, favoring bioluminescence over moonlight and starlight as a selective force in determining λ_{max} position, would also favor bioluminescence over twilight. But there is an important difference in this last comparison. Moonlight and starlight would select for spectral positions different from that selected for by bioluminescence, and so a conflict would exist. Twilight, on the other hand, would select for essentially the same spectral position as bioluminescence, so that the two would act in concert (see below).

If scotopic visual pigments with spectral positions slightly above 500 nm are optimally located to detect bioluminescence in Californian coastal waters, one can see why such pigments occur there in fishes exposed to nocturnal predators. But questions remain concerning why fishes apparently less threatened are consistent in having scotopic pigments positioned slightly under 500 nm. Why are these pigments not loosely positioned above, as well as below, the optimum location? The answer to this question might lie in ancestral relationships. In grouping the Californian fishes according to whether their geographical affinities are tropical or temperate (Table 4), our concern was with current relationships. In fact, all these fishes belong to groups that stem from tropical origins (Berg 1940). The radiation of acanthopterygian[5] fishes from a relatively few ancestral forms early in the Cenozoic (Patterson 1964; Romer 1966) has been related (by Hobson 1974) to the concurrent development of modern coral reef communities (Newell 1971). And we have seen that conditions under which coral reefs flourish, compared with conditions in temperate Californian waters, favor in fishes' scotopic visual pigments that are more sensitive to slightly shorter wavelengths. The mean λ_{max} of 492 nm that Munz and McFarland (1973) found in the scotopic pigments of coral-reef fishes, compared with the values around 500 nm that characterize Californian fishes, is consistent with the fact that water around coral reefs is generally clearer and more transparent to blue light than water around Santa Catalina (Figure 2). The extent that λ_{max} values of scotopic pigments in Californian coastal fishes have shifted toward the green from what may have been ancestral positions near 490 nm, and, especially, have become located slightly above 500 nm (the optimal position in California), may roughly measure the relative strength of nocturnal or crepuscular predation pressures on each species in these greener waters.

The argument that scotopic pigments may be positioned to detect bioluminescence can be extended to coral reef fishes. Our calculations show that visual pigments with different λ_{max} values would trap percentages of the light from *Noctiluca miliaris* as follows: P450 nm = 62%, P475 nm = 94%, P490 nm = 100%, P500 nm = 99%, P525 nm = 93.5%, P550 nm = 79%. Although the peak is broad, the central wavelength for maximum absorption at zero range would be near 495 nm (Figure 14), which is close to the λ_{max} of 492 nm in the scotopic pigments of coral-reef fishes. And as distance from the source increases the match becomes even better (Figure 15).

Twilight or Bioluminescence?

Whether the clustering and spectral position of visual pigments in warm-temperate and tropical reef fishes is the result of natural selection, or is simply fortuitous, is a complex question. If, as we believe, these features have been refined by intense selection pressures from predators, it remains problematical whether the advantage lies in detecting bioluminescence, or in enhancing photoabsorption during twilight—as suggested by the Twilight Hypothesis. Indeed, both may be important. The scotopic pigments have spectral positions that would be effective in both functions, and the benefits of one would complement the other. Unquestionably, there has been ample time to influence evolution. Bioluminescent plankton have existed since before the first fishes (Seliger 1975), and so has twilight's unique spectrum. Because fishes have experienced these features throughout their history, the slightest favorable adjustment could have been adaptive. Although a 5-10 nm shift in λ_{max} position would improve photoabsorption by no more than a few percentage units, even this could have been meaningful. And if selection pressures to detect bioluminescence have, in fact, acted in concert with those to enhance crepuscular vision, which to us seems likely, then their combined impact certainly would have been a powerful evolutionary force.

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[5] All fishes considered in this paper have been included among the acanthopterygians, or spiny-finned teleosts, although one, *Atherinops affinis*, would be relegated by some systematists (e.g., Greenwood et al. 1966) to another group

(NMFS), NOAA, typed the manuscript, and Susan Smith, Southwest Fisheries Center Tiburon Laboratory, NMFS, NOAA, drew Figure 1. Portions of this study were supported by N.I.H. Research Grant EY-00323 from the National Eye Institute.

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THE SPAWNING ENERGETICS OF FEMALE NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

J. Roe Hunter and Roderick Leong[1]

ABSTRACT

The seasonal pattern in incidence of postovulatory follicles in northern anchovy females indicated that they spawn about 20 times per year. The maturation rates of females in the laboratory indicated that they were capable of maturing a spawning batch of eggs at weekly intervals. Examination of the egg size frequency distributions in sea-caught specimens indicated that vitellogenesis and egg maturation continued until the last spawning. We evaluated for northern anchovy the fat-water balance, caloric values of tissues, annual fat cycle, seasonal changes in egg weight, total calories present in a mature ovary, batch fecundity; and determined in the laboratory the gross caloric conversion efficiency (12.8%). These measurements indicated that the caloric equivalent of only two spawning batches are present in a mature ovary at any time and that two-thirds of the annual cost of 20 spawnings could be supplied by fat stores. Estimates of annual reproductive effort (egg calories/ration calories × 100) ranged from 8% for 1 year to 11% for 3-year-old females. A daily ration of copepods equivalent to 4-5% of female wet weight per day is required to support the annual cost of growth and reproduction.

Histological evidence indicated that female northern anchovy, *Engraulis mordax*, spawned about once a week in February 1978 (Hunter and Goldberg 1980) and at 7-10 d intervals from late January through the middle of April 1979 (Hunter and Macewicz 1980). Egg and larva survey data indicate that some spawning occurs throughout the year, although about 50% of the annual production of northern anchovy larvae occurs during the peak months of spawning (February to April) (Lasker and Smith 1977). These findings indicate that northern anchovy females spawn many times per year. Thus, the annual fecundity of northern anchovy is higher than originally suspected by MacGregor (1968) and may be regulated by availability of food. Energy regulation of fecundity has been suggested for other marine fish stocks and could be important as a density-dependent population regulation mechanism (Bagenal 1973).

The objectives of this study were: to validate recent work on northern anchovy spawning by determining if such a high frequency of spawning is developmentally and energetically possible; to estimate the annual energy cost of reproduction; and to discuss the sources of variation. We estimated the average number of spawnings by northern anchovy females in a year and tested the hypothesis that they are capable of maturing eggs at the required rate. We considered the energy cost of reproduction, factors that affected variation in costs, and related reproductive costs to fat stores. Finally we estimated the annual reproductive effort (egg cal/ration cal). In addition to data collected specifically for this study, we used data available at the Southwest Fisheries Center (SWFC), La Jolla, Calif., including many unpublished sources.

METHODS

Field Data

To estimate the annual number of spawnings by northern anchovy, we used the data of Hunter and Goldberg (1980) and Hunter and Macewicz (1980) on the incidence of 24-h-old postovulatory follicles. The proportion of mature females with 24-h-old postovulatory follicles was considered equivalent to the fraction of females spawning per day during a cruise (Hunter and Goldberg 1980). All samples were taken in the Southern California Bight in 1977-79; the number of females analyzed per cruise was 148 from March 1977; 14 from September 1977; 295 from February 1978; 395 from January-February 1979; 557 from March-April 1979; and 33 from June 1979. Data were plotted at the mid-date for the cruises which were 10-22 d long.

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To estimate the rate of egg maturation required for weekly spawning, we used the frequency distributions of egg size in mature northern anchovy ovaries of females taken at sea. We measured distributions in 10 females taken in the Southern California Bight in February 1979, and in 6 taken in Monterey Bay in March 1979 by Hunter and Macewicz (1980). Five of the females from the Southern California Bight had 24-h-old postovulatory follicles indicating spawning had occurred on the day before they were captured, and the other five were mature without evidence of recent spawning. The ovaries of the six females from Monterey were highly atretic and in postspawning condition, but had yolked eggs (Hunter and Macewicz 1980). This latter group was used to illustrate the condition of ovaries at the cessation of spawning. Our method of measuring the egg size-frequency distributions was similar to that of MacGregor (1968). We counted and measured to the nearest 0.05 mm all eggs >0.05 mm (major axis) in a weighed sample of the ovary.

Seasonal changes in fat content of female northern anchovy were calculated using the original data summarized by Lasker and Smith (1977). Their samples were taken at roughly monthly intervals from February 1965 to June 1967 ($n = 593$). Their data, supplemented by additional data ($n = 338$) taken in the summer and fall of 1979, were used to estimate the relation between wet weight without gonad (W) and fat content (F) and dry weight (without fat) (D). The multiple regression equation for this relation was

$$W = -0.018 + 0.320\,F + 5.469\,D \qquad (1)$$

where all variables are in grams, $r^2 = 0.969$, and $n = 981$. This equation permitted calculation of wet weight of northern anchovy females after fat gain or loss. Wet weight changes only slightly with fat loss because water content increases as fat decreases (Iles and Wood 1965) (Table 1). The same data were used to establish the relation between dry weight (without fat) (D) and standard length (L) where

$$\log_{10} L = 0.313 \log_{10} D + 1.930, \qquad (2)$$

$r^2 = 0.974$. Thus, wet weight can be estimated for northern anchovy of any standard length given the fat content.

Ahlstrom[2] measured the major and minor axes of 50-150 northern anchovy eggs taken in each of 58 standard ichthyoplankton tows (Smith and Richardson 1977) along the coast of California and Baja California in 1955, 1956, 1957, and 1965. These data, combined with an additional 30 tows (100 eggs measured/tow) taken in the same region in 1969, were used to estimate seasonal changes in the size of northern anchovy eggs. We calculated monthly mean egg dimensions for the combined data; number of tows per month varied from 9 to 16 (February-July) and from 1 to 4 in the period of low egg abundance (August-December). We calculated the mean volume of the eggs per month from average egg dimensions using the equation for a prolate spheroid. The volume (V) in cubic millimeters was converted to dry weight (E) in milligrams with the relation established in the laboratory using freshly spawned eggs

$$E = 0.0012 + 0.0930\,V \qquad (3)$$

where $r^2 = 0.646$ and $n = 32$.

Laboratory Data

Three groups of northern anchovy of 1,200-1,300 fish each were matured in the laboratory to measure the rate of ovarian maturation and to estimate gross growth efficiency. The fish were

TABLE 1.—Relationship between fat-free dry weight or length and wet weight for northern anchovy at the average seasonal minimum and maximum fat content. Relationships calculated from regressions; all body weights are without gonads.

Standard length[1] (mm)	Fat-free dry weight (g)	Wet weight and water content at minimum (15%)[2] fat content			Wet weight and water content at maximum (41%)[2] fat content		
		Fat (g)	Wet weight[3] ±95% C.I.	Water[4] (%)	Fat (g)	Wet weight[3] ±95% C.I.	Water[4] (%)
106	2.000	0.353	11.03±0.19	79	1.390	11.36±0.11	70
118	2.891	0.510	15.96±0.13	79	2.009	16.44±0.18	70
131	4.000	0.706	22.08±0.12	79	2.780	22.75±0.35	70

[1] From Equation (2) in text.
[2] Percentage of the dry weight including fat.
[3] From Equation (1) in text; 95% confidence intervals calculated using Gauss multipliers (Snedecor and Cochran 1967).
[4] $[W - (D + F)/W] \times 100$, where W = wet weight without ovary, D = fat-free dry weight, and F = weight of fat.

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[2] E. H. Ahlstrom, Southwest Fisheries Center, NMFS, NOAA, La Jolla, CA 92038, unpubl. data, 1979.

purchased from bait dealers from September to October in 1977 and 1978 and held in circular tanks 4.6 m in diameter × 1 m deep (volume 16.6 m^3) with a fresh seawater inflow of 20 l/min. The fish were exposed to the natural photoperiod but were shielded from direct sunlight. They were fed a ration of Oregon Moist Trout Pellets[3] 6 d/wk. The pellets were dispensed with an automatic feeder over a 4-5 h feeding period beginning at 0800 h (Leong 1971).

To estimate the rate of egg maturation (group 1), 8-12 females were sampled twice weekly for 6 wk. The ovaries of nearly all females were immature (no yolked oocytes) when sampling began; the mean standard length (SL) of females was 112.4 mm increasing to 116.4 mm in 6 wk. The fish were held at ambient temperatures which ranged from 17.9° to 22.0° C and averaged 19.7° C; daily temperatures closely followed those taken at the Scripps Institution of Oceanography pier. We measured standard length, wet weight, and determined the frequency distribution of egg sizes within the ovary for each female sampled. We used as a measure of the state of sexual maturity, the mean size of eggs (major axis) within the most advanced spawning batch. The number of eggs within a batch was calculated from the wet weight of the female using the batch fecundity equation of Hunter and Macewicz (1980)

$$\log_e T = 4.248 + 1.620 \log_e W. \qquad (4)$$

(Equation corrected for bias in taking the antilog; Beauchamp and Olson 1973), where T = total number of eggs in a spawning batch and W = female wet weight (without ovary) in grams.

To measure growth efficiency, two groups (groups 2 and 3) were held under similar tank conditions, but were sampled at 2-wk intervals beginning at the end of November and ending in mid-February. Group 2 was in captivity for about 1 mo and group 3 for 2 wk prior to sampling. Group 2 was held at 15.6° C while group 3 was held at ambient temperatures which ranged from 15.2° to 17.0° C and averaged 16.0° C. Mean standard length of fish in groups 2 and 3 was 107.2 mm at the beginning and 121.4 mm at the end of the experiment.

The stomach contents of each fish sampled from groups 2 and 3 were weighed and used to determine the mean ration for the experiment. The ration was calculated from the equation

$$R = r \cdot s \cdot t + S_e \qquad (5)$$

where R = ration, expressed as wet weight food consumed/wet weight fish (in grams); r = rate of gastric evacuation (dashed line, Figure 1); s = average weight of food in stomach/fish weight during the period of gut filling (solid line, Figure 1); t = duration of feeding (4 h, group 2; 5 h, group 3); and S_e = weight of food in stomach/fish weight

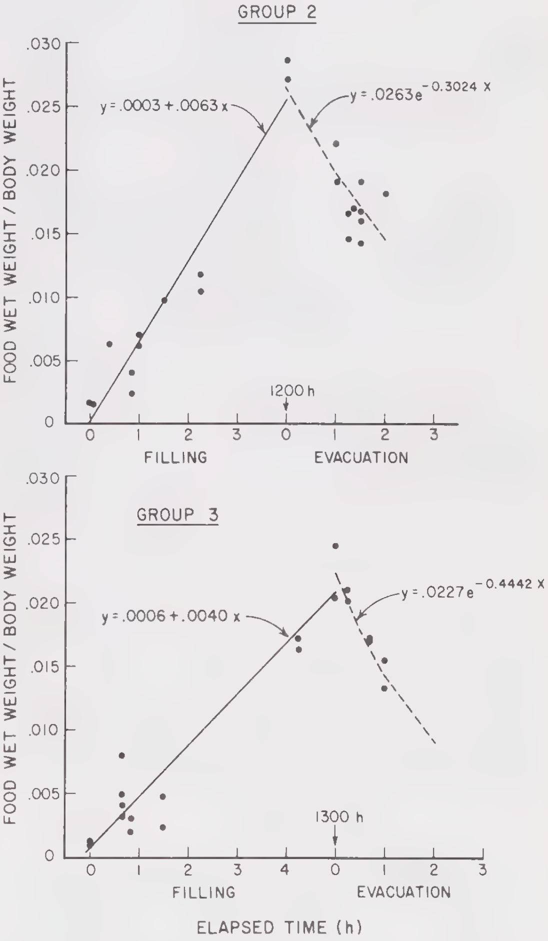

FIGURE 1.—Rate of stomach filling and gastric evacuation in two groups of northern anchovy fed Oregon Moist Trout Pellets. Weight of stomach contents expressed as a proportion of fish weight; each point is mean for 8-12 fish; feeding began at 0 h (filling) and ended at 0 h (evacuation) (arrow); time of day when feeding ended is above arrow. Daily ration calculated from these data was 4.4% body weight/d, group 2; and 4.6% body weight/d, group 3.

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[3] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

at end of feeding period. Similar functions have been used by Tyler (1970), discussed and used by Eggers (1977), and discussed by Elliot and Persson (1978). The daily pattern of feeding and evacuation and the data used to calculate the parameters for the ration equation are given in Figure 1. We use an exponential equation to estimate rate of gastric evacuation (r) because it is required by theory and the above model and use a linear regression equation for gut filling because the equation is used only to provide an empirical estimate of the mean stomach contents (s) during feeding.

The mean ration for a feeding day was 0.0437 g/g body wet weight (group 2) and 0.0462 g/g body wet weight (group 3); these values were multiplied by the mean wet weight of fish sampled (18.6 g, group 2; 17.6 g, group 3) to express the ration in terms of the average fish weight in each experiment. This value was adjusted by the ratio, total number of feeding periods/duration of the experiment (days) (ratio = 59/69, group 2; 67/78, group 3), to adjust the ration for days when no feeding occurred. This daily ration for the experiment was converted to calories by multiplying by 0.656 (average ratio of dry to wet weight for stomach contents of northern anchovy fed Oregon Moist Trout Pellets) and by 4,912, the caloric value per gram for this food (Table 2). The daily ration for fish in group 2 was 2,238 cal/d and was 2,245 cal/d for fish in group 3.

TABLE 2.—Mean calories per gram dry weight of various northern anchovy tissues and food.

Tissues or food	*n*	Mean calories	SD
Anchovy fat	4	9,227	40
Anchovy eggs (including fat)	4	5,450	90
Whole female anchovy, less ovary (fat free)	11	4,129	176
Anchovy ovary (fat free)	29	4,960	79
Anchovy ovary with 18%[1] fat	—	5,710	—
Oregon Moist Trout Pellets	4	4,912	214

[1] 18% is the mean fat content of northern anchovy ovaries; caloric value was calculated from the values for fat and fat-free ovary.

Dry weight and fat content of northern anchovy were determined for the first and last samples of groups 2 and 3. Fish were dried in an oven at 60° C until constant weight and fat extracted using Soxhlet extraction with chloroform-methanol (Krvarić and Mužinić 1950).

Caloric values of northern anchovy oil, newly spawned eggs, ovaries and whole females (without ovaries), and Oregon Moist Trout Pellets were estimated using a Parr bomb calorimeter and standard techniques (Table 2). Laboratory fish were used for all measurements except for the caloric value of northern anchovy oil where sea-caught specimens were used.

SPAWNING FREQUENCY AND RATE OF EGG MATURATION

Number of Spawnings per Year

We plotted the fraction of females spawning per day (females with 24-h-old postovulatory follicles) as a function of sampling date to estimate the number of spawnings produced by female northern anchovy in 1 yr. The seasonal change in the fraction of females spawning followed the seasonal change in the average relative larval abundance for 1953-60 (Lasker and Smith 1977) (Figure 2). The fraction of females spawning was the highest during peak spawning months and declined to zero by September. In peak spawning months the percentage of mature females spawning per day was 16-14%, indicating that individual females spawned every 6-7 d. The seasonal decline in the fraction of females spawning per day could be caused by an increase in the interval between spawnings in individual females, or by a complete cessation of spawning by an increasingly larger proportion of the population, or by a combination of these events.

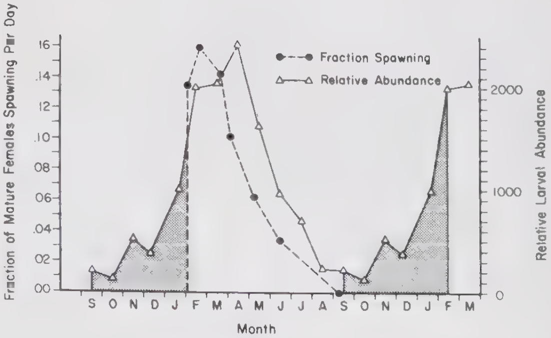

FIGURE 2.—Fraction of mature northern anchovy females from the Southern California Bight spawning per day during various months (dots). Fraction calculated from incidence of females with 24-h-old postovulatory follicles (Hunter and Goldberg 1980; Hunter and Macewicz 1980). Triangles indicate relative larval abundance per month from 1953 to 1960 (Lasker and Smith 1977). Shaded areas indicate months where spawning fraction was not estimated; total spawnings per year by northern anchovy females was estimated from areas under the two curves (see text).

The area under the curve for fraction of females spawning per day is an estimate of the number of spawnings produced per female from February to September. This calculation indicated that each mature female northern anchovy spawned on the average 15 times between February and September. The number of spawnings that occurred in October-January (shaded area, Figure 2) had to be estimated indirectly because no ovary samples existed. We assumed that the number of spawnings was proportional to the relative larval abundance in October-January, adjusted by the ratio of the areas under the spawning fraction and larval abundance curves for Feburary to September. This calculation indicated that about five spawnings would have had to occur in October-January to account for the abundance of larvae in that period; this brings the total number of spawnings for female to 20 for the year.

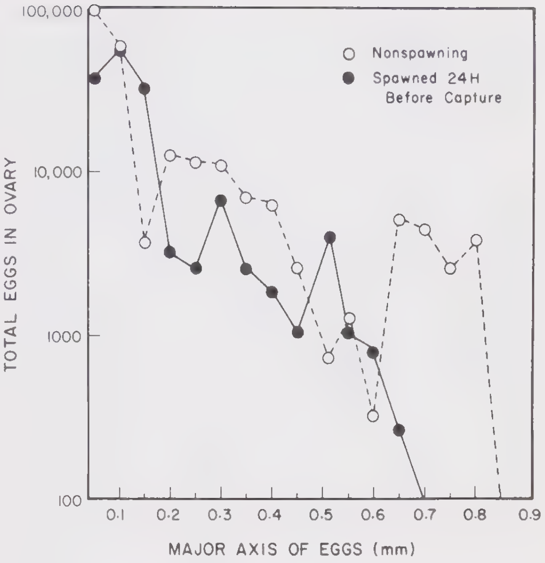

FIGURE 3.—Total eggs in ovary ($\log_{10}$ scale) as a function of the major egg axis for a 20.2 g female northern anchovy (ovary-free weight) captured 24 h after spawning and for a 25.3 g female, showing no evidence of recent spawning (nonspawning). Smallest eggs measured were 0.05 mm; measurements were made in increments of 0.05 mm. Females were captured in January to February 1979 in the Southern California Bight.

Form of Frequency Distribution of Egg Size

The form of the egg size distribution in mature northern anchovy ovaries is illustrated for a female taken 24 h after spawning and a mature female without evidence of recent spawning (nonspawning) (Figure 3). Ovarian egg size distributions typically resemble these except for females with hydrated eggs, where the hydrated eggs stand out as a discontinuous group of large eggs. In mature females (without hydrated eggs) the egg size distributions are continuous and typically have one or two modes as illustrated. In the nonspawning female a major mode of large yolked eggs existed between 0.6 and 0.8 mm (major egg axis) and in the spawned female the first modal group occurred at about 0.5 mm. Eggs <0.2 mm are the most abundant size class in both ovaries. These small eggs, also abundant in immature ovaries, form part of the reservoir of immature unyolked eggs which are matured during each spawning season.

Yolk appears in the egg when the major axis of the egg reaches about 0.4 mm. The ovary of the spawned female (20.2 g) in Figure 3 contained 9,384 yolked eggs, whereas that of the nonspawning female (25.3 g) contained 26,761 yolked eggs. The batch fecundity equation (Equation (4)) predicts a batch size of 9,110 eggs for the spawned female and 13,120 eggs for the nonspawning female. Hence, about one spawning batch of yolked eggs existed in the spawned female and about two in the nonspawning female. If a female were to spawn more than a few times in one season, it would have to mature and yolk many of the small unyolked eggs in the ovary. If spawning were to occur at weekly intervals for months, this would be a continuous process.

Rate of Egg Maturation Required for Continuous Production of Eggs Compared With Laboratory Maturation Rate

For northern anchovy to continually mature and add yolk to a series of egg batches, the abundance of egg sizes in the ovary must vary inversely with the rate of egg maturation. Thus, a hypothetical curve for the rate of maturation of anchovy eggs can be constructed from the average size of eggs in each potential spawning batch within an ovary, if the time between batches or spawning frequency is known. This hypothetical rate can then be compared with the rate of egg maturation in the laboratory to determine if the predicted rate is possible.

To conduct this test for northern anchovy, we partitioned the total number of eggs in the ovary of 10 sea-caught fish into successive spawning batches (starting with the largest eggs) and calculated the mean major axis of eggs in each successive batch. The number of eggs per batch was estimated from the wet weight of the females using the batch fecundity Equation (4).

As might be expected, the mean major axis of eggs in each of the potential spawning batches for the five females taken 24 h after spawning was about one spawning batch out of phase from the five nonspawning fish (Figure 4, upper). When the most advanced spawning batch of the recently spawned group was lagged by one spawning interval, the function was the same for both groups (Figure 4, lower) and similar to data on "nonspawning females" in Hunter and Goldberg (1980). The lower curves indicate that about four spawning batches of eggs >0.15 mm exist in the ovary of females near spawning condition. Hunter and Goldberg (1980) determined for 38 mature nonspawning females that the mean size of eggs in the most mature batch was 0.59 mm; and in the 5 females in the present analysis, the mean size was 0.71 mm. Thus a batch of eggs of 0.15 mm mean size major axis would have to reach about 0.6-0.7 mm in about 4 wk (28 d) if females were to spawn five or more times at weekly intervals.

The ovaries of all laboratory females were immature when the maturation experiment began (elapsed time = 0, Figure 5) although the mean size of eggs in the most advanced spawning batch was quite variable among females (mean egg size ranged from 0.13 to 0.48 mm). To illustrate the rate of ovarian maturation we used the average of the mean egg size in the spawning batch of individual females (Figure 5). The rate of maturation of ovaries in the laboratory group was similar to that predicted from egg size frequency distributions of wild fish, if one assumes spawning in the sea occurs weekly (line, Figure 5). The average of the mean size of eggs in the most advanced spawning batch was 0.15 mm after the first week of the experiment and was 0.62 mm 4 wk later. Thus maturation of eggs from 0.15 to 0.62 mm occurred in four wk and is about the same as the theoretical estimate based on egg size distributions in sea-caught specimens. This demonstrates that the rate of egg maturation required for continuous production of egg batches

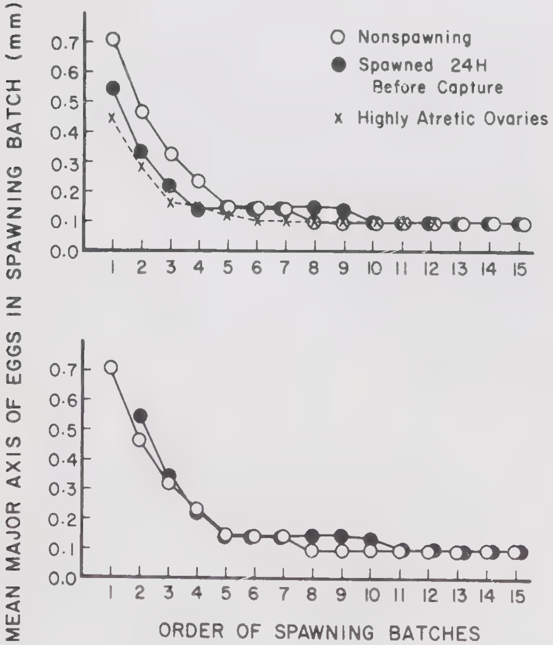

FIGURE 4.—Mean major axis of eggs in successive spawning batches within the ovary of northern anchovy. Number of eggs per batch estimated for each female from Equation (4). Numbers on abscissa indicate order of spawning batch with 1 = the most advanced batch. Circles are means of five nonspawning females (no evidence of recent spawning), and dots are means for five females having spawned within 24 h (females taken in the Southern California Bight); the X's are means for six females with highly atretic ovaries taken in Monterey Bay in 1979. The lower panel illustrates the correspondence between average egg size in successive batches in nonatretic ovaries when recently spawned females are lagged by one spawning batch interval. Only the 15 batches containing the largest eggs are shown.

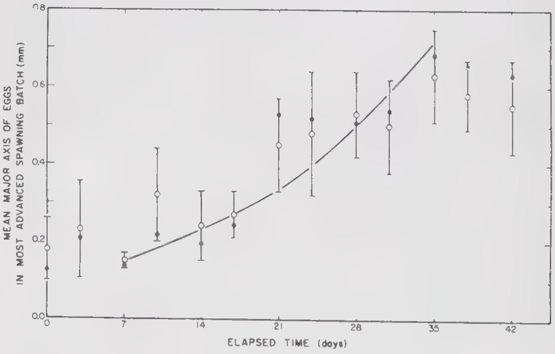

FIGURE 5.—Maturation of eggs in the most advanced spawning batch of laboratory-held northern anchovy as a function of elapsed time. Maturity is achieved when average egg size in batch attains 0.6-0.7 mm. Circles are averages of the mean size of eggs in the most advanced spawning batch of females sampled on a particular day, dots the median, and bars are ±2 SE. Number of eggs used to calculate the mean for each female was determined using Equation (4). The solid line is hypothetical maturation rate of egg batches from 0.15 mm (major egg axis), assuming females spawn at weekly intervals; the line is derived from data in Figure 4.

at 7-10 d intervals occurs in the laboratory and could occur in the sea. In addition, the forms of the theoretical and the laboratory maturation curves were similar, with maturation of small unyolked eggs being much slower than that of larger yolked eggs.

Cessation of Spawning

An assumption of some fecundity studies of multiple spawning fishes is that all eggs to be spawned in a season are yolked at the beginning of the season and spawning ends when these yolked eggs are depleted. The preceding analysis indicated that yolking of eggs from the reservoir of small unyolked eggs is a continuous process in northern anchovy. In this section we determined whether spawning ceases because of a lack of eggs of an appropriate size for maturation. We compared egg size-frequency distributions from six females with highly atretic ovaries with those of reproductively active females. Although the ovaries of the six females contained yolked eggs, they were highly atretic and judged to be in postspawning condition, using histological criteria presented by Hunter and Macewicz (1980).

The form of the line relating the mean major axis of eggs to successive spawning batches (dashed line, Figure 4, upper) was similar in form to those of the other groups. The eggs in the most advanced spawning batch were smaller (0.45 mm) in atretic ovaries than in those of females that had spawned 24 h before capture (0.55 mm). Hunter and Goldberg (1980) showed that the mean major axis of the most advanced eggs (excluding hydrated eggs) was 0.46 mm in females captured on the night of spawning. This value is very close to the mean for highly atretic ovaries. Thus, oocyte maturation, at least in these six females, probably continued up to the time of the last spawning, whereupon maturation ceased and the remaining oocytes became atretic. Spawning did not cease because of lack of yolked eggs; the atretic ovaries of these six females had the same distribution of egg sizes as any female ovary immediately after spawning.

ENERGY COST OF SPAWNING

We consider here three variables affecting the cost of reproduction: Number of eggs in a spawning batch, size of eggs, and the energy existing in a mature ovary. Factors not considered include the metabolic costs of egg maturation and reproductive behavior and variation in the caloric content of eggs.

Number of Eggs

The spawning batch fecundity (number of hydrated eggs) of northern anchovy varies exponentially with female weight (Equation (4)). Similar to many other fishes (Bagenal 1973), fecundity among females of the same size or weight is highly variable. Variability may be caused by variations in egg size, food availability, and number of previous spawnings within the season.

Feeding conditions may not greatly affect batch fecundity in northern anchovy. Females matured in the laboratory (groups 2 and 3) were fed a high ration and grew about four times faster than those in the sea, yet the batch fecundity was about the same as field-caught specimens, which consume a lower ration (Table 3). Although the laboratory females had not begun spawning, their batch fecundity was similar to that of fish taken in the sea between January and April. This indicates that the average batch fecundity may not change over the first months of spawning. The fact that fecundity of females captured in March-April 1979 was about the same as that for January-February 1979 (Hunter and Macewicz 1980) also supports

TABLE 3.—Comparison of the batch fecundity of northern anchovy females matured in laboratory and in the sea within two weight classes.

Weight class (g)	Locality	n	Mean weight (without ovary) (g)	Batch fecundity (total eggs): Mean ± 2 SE	Batch fecundity (total eggs): Estimated for mean weight from fecundity equation for sea-caught female[1]
15-19.9	Laboratory[2]	38	17.9	8,910 ± 1,210	7,420
	Sea[3]	17	16.7	6,800 ± 1,150	6,690
20-24.9	Laboratory[2]	12	22.8	11,900 ± 950	11,100
	Sea[3]	21	22.6	10,400 ± 1,540	10,900

[1] From Equation (4) (Hunter and Macewicz 1980); intercept increased by 0.0647 ($\frac{1}{2}s^2$) to adjust for bias in taking antilog (Beauchamp and Olson 1973).

[2] Batch fecundity = number eggs in most advanced mode in ovary where mean egg size $\geqslant$0.65 mm (major axis; eggs not hydrated).

[3] Batch fecundity = number of hydrated eggs in females without new postovulatory follicles (Hunter and Goldberg 1980; Hunter and Macewicz 1980).

this view. We conclude that, at least over the first few months of spawning, the mean number of eggs per spawning batch may be independent of past spawning history.

Size of Eggs

The size of spawned northern anchovy eggs varies seasonally as do those of other clupeoid fishes (Blaxter 1969; Ciechomski 1973; Le Clus 1979). Smith and Richardson (1977) demonstrated that the major axes of northern anchovy eggs spawned in February 1972 were larger than those of eggs spawned in August 1972 ($P = 0.05$). The seasonal trend in dimensions of northern anchovy eggs is illustrated in Figure 6 (upper). The dry weight of eggs (calculated from their volume (Equation (3)) varies by about 20% over the spawning season; thus, females could produce about five more spawnings/yr at the minimum egg size than at the maximum with no increase in energy demand. The seasonal trend in egg dry weight is similar to the relative larval abundance (shaded area of Figure 6), with the largest eggs produced in February to April when most of the spawning occurs and the smallest eggs late in the summer when the least spawning occurs. Several possible explanations exist for the seasonal trend in egg size. Females may produce smaller eggs as the spawning season progresses or, alternatively, large females which begin spawning earlier may produce larger eggs than small females. Regardless of the mechanism, it probably is adaptive to produce larger eggs early in the spawning season when water temperatures are cooler since the advantage falls to larger eggs as water temperature declines, because incubation periods are longer (Ware 1975).

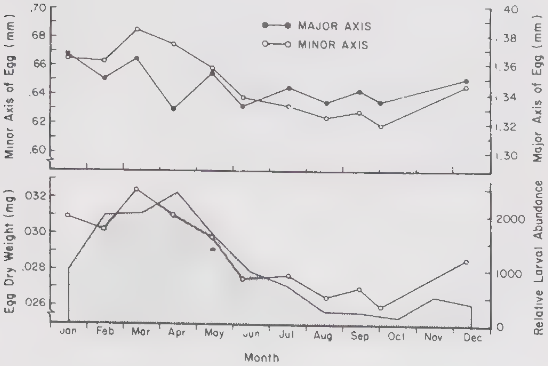

FIGURE 6.—Mean size of northern anchovy eggs taken in routine plankton tows by month. Upper, mean major and minor axes of eggs; lower, mean weight of eggs calculated from average dimensions of eggs given in upper figure using Equation (3); shaded area is the relative larval abundance for years 1953-60, from Lasker and Smith (1977).

Maturation of Eggs

Northern anchovy eggs <0.1 mm are spherical; they become oblate spheroids between 0.1 and 0.25 mm (major axis) and thereafter retain the same proportionality between axes through hydration and spawning (Figure 7, upper). Hydration of the spawning batch of eggs (rapid uptake of fluid) begins about 12 h before spawning (Hunter and

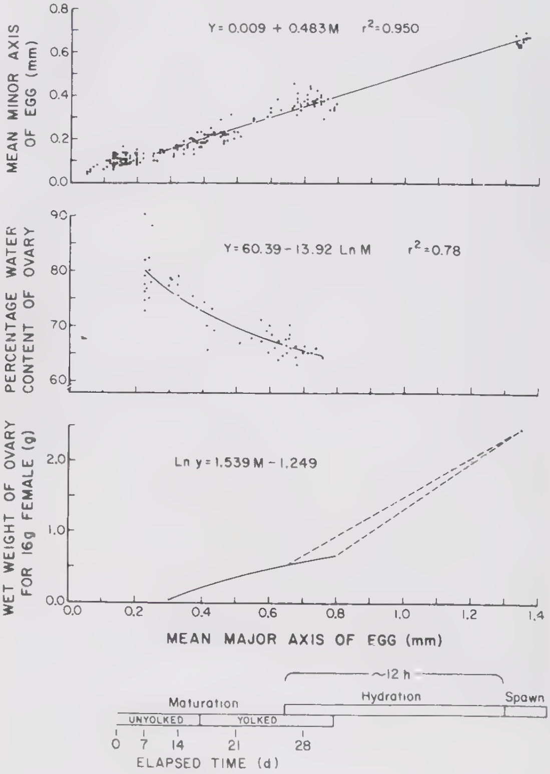

FIGURE 7.—The mean length of the minor egg axis (upper), water content of the ovary (middle), and ovary wet weight of a 16 g northern anchovy female calculated from Equation (6) (bottom), as functions of the mean major egg axis of eggs in the most advanced spawning batch (natural logarithms were used). Original data for Equation (6) (solid line, bottom) given in Hunter and Goldberg (1980); dashed lines indicate the range of egg sizes that may hydrate; and they converge at the average weight of a hydrated ovary in a 16 g female. Time scale on abscissa is based on hypothetical rate of egg maturation required for weekly spawning (see Figure 4).

Macewicz 1980), resulting in a rapid increase in ovary wet weight (Figure 7, lower) but no change in dry weight (Le Clus 1979). The mean size of eggs in a spawning batch, just before hydration, ranges from 0.6 to 0.8 mm; eggs >0.8 mm nearly always show histological signs of hydration. The average size of eggs that are hydrated would be expected to vary since the size of spawned eggs is variable.

The wet weight of the ovary (G) increases during maturation and is a function of the mean major axis of the eggs in the most mature spawning batch (M) and female wet weight without ovary (W); in northern anchovy this function is expressed as

$$\log_e G = -4.213 + 1.069 \log_e W + 0.555\, M \log_e W \qquad (6)$$

(Hunter and Goldberg 1980) (Figure 7, lower). The water content of the ovary of laboratory females (group 1) declined during maturation from 80 to 65% just before hydration (Figure 7, center). The fat content did not change significantly over the maturation period; mean ovarian fat content of laboratory-matured northern anchovy was $18.6 \pm 1.2\%$ (± 2 SE of mean, $n = 41$) of ovary dry weight. As the fat content did not change, the caloric value of ovarian tissue can be considered to be constant at 5,710 cal/g dry weight (Table 2).

Using Equation (6), caloric values (Table 2), and water content of ovary (Figure 7), we estimate the ovary of a 16.4 g female contains 933 cal just after spawning when the mean major axis of most advanced eggs = 0.46 mm (Hunter and Goldberg 1980). The spawning batch of a 16.4 g female contains 6,500 eggs or 1,066 cal (from Equation (4)). Thus, just before spawning the ovary contains about 2,059 cal and the most advanced spawning batch constitutes about 52% of the calories in the ovary (documentation given in Table 4). Similar calculations can be made using the volume of eggs in the ovary and egg dimensions given in Figure 7 (upper) or by calculating the wet weight of the ovary at 0.46 mm egg major axis (after spawning) and at 0.81 mm egg major axis (at onset of hydration) using Equation (6). All calculations yield similar results when converted to dry weight or calories, i.e., about one-half of the calories in the ovary are lost in one spawning. We conclude that the calories invested in a mature ovary are small relative to the total reproductive cost of 20 spawnings.

ANNUAL FAT CYCLE AND SPAWNING

As the caloric equivalent of only two spawnings exists in the ovary at one time, northern anchovy must use energy stored in other tissues and food income to support reproduction. Lasker and Smith (1977) showed that the fat content of northern anchovy, like many other clupeoids (Blaxter and Holliday 1963; Shul'man 1974) varies seasonally. The fat accumulates in the body rapidly between April and July, matching the annual spring bloom of zooplankton (Lasker and Smith 1977). It usually remains high through December and then declines to a minimum between February and May (Figure 8). The decline in fat occurs during the months of maximum spawning. Thus, fat stored

TABLE 4.—Reproductive characteristics for the average female northern anchovy.

Item	Value	Explanation and data source
Weight and fecundity:		
Mean female wet weight, less ovary	16.4 g	For 1978 and 1979 (Hunter and Macewicz 1980)
Ovary wet weight after spawning[1]	.601 g	Equation (6) where M = 0.46 mm
Ovary dry weight after spawning[1]	.174 g	Percentage water in ovary from Figure 7 (center)
Number of eggs in one spawning batch	6,500 eggs	Equation (4)
Number of eggs spawned/yr	130,000 eggs	Assume 20 spawnings (Figure 2)
Dry weight one spawned egg	.0301 mg	Mean of monthly dry weight: (Figure 6) weighted by relative monthly larval abundance (Lasker and Smith 1977)
Caloric content of ovaries and spawn:		
Calories in one spawning batch	1,066 cal	Caloric value of eggs = 5,450 cal/g (Table 2)
Calories in ovary after spawning	993 cal	Caloric value of ovary = 5,710 cal/g (Table 2)
Calories in ovary just before spawning	2,059 cal	
Percentage of calories in ovary lost in one spawning batch	52%	
Daily spawning cost during peak spawning months	152 cal/d	Assume spawning interval = 7 d
Spawning related to fat stores:		
Maximum fat in body	2.009 g	Equation (1) where 41% of dry weight = fat
Minimum fat in body	.510 g	Equation (1) where 15% of dry weight = fat
Total fat stores	13,831 cal	Caloric value of fat = 9,227 cal/g (Table 2)
Fat stores in spawning batch equivalents	13 batches	

[1] Females with postovulatory follicles < 24 h old.

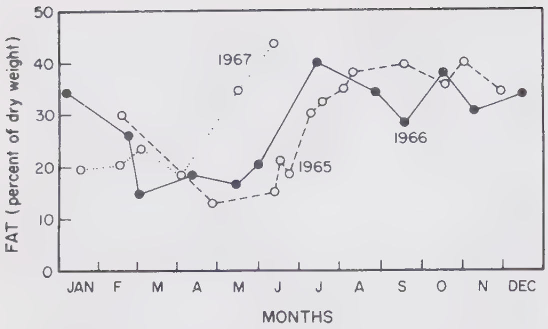

FIGURE 8.—Annual fat cycle of northern anchovy. Fat content expressed as a percentage of dry weight for various months in 1965, 1966, and 1967. Data from Lasker and Smith (1977).

from the previous spring and summer may be used the following year to support reproduction. Fat stores may not be used directly to promote egg production, which are largely protein, but rather to provide energy needed for metabolism, permitting energy from food to be used for egg maturation.

We calculated the number of spawnings that could be financed by the annual decline in fat stores, assuming that this energy or its equivalent is used for reproduction. We used the average minimum and maximum fat level for the 3 yr (Table 5) to estimate the grams of fat annually available for reproduction. Using the dry weight, fat, and wet weight relation (Equation (1)), we calculate that a 16.4 g female would store annually 13,831 cal of fat (Table 4) which is equivalent to 13 spawning batches. Thus, about two-thirds of the annual cost of egg production can be accounted for by the annual decline in fat stores.

The rate of increase in fat in the spring was similar in the 3 yr (1965-67) although the timing of the onset varied by 2-3 mo. The maximum rate occurred in the late spring or summer over a period of about 63 d (Table 5). Nearly all fat stores were accumulated over this period; on the average fat increased from 16.5 to 40.5% of the dry weight over the 63 d. Thus, calories would accumulate in a 16.4 g fish at a rate of about 200 cal/d or the caloric equivalent of one spawning batch would be stored about every 5 d.

TABLE 5.—Maximum and minimum fat content of female northern anchovy from Southern California Bight in 1965-67.[1]

	Fat content (% dry weight)				Period of maximum rate of increase in fat stores	
	Minimum		Maximum			
Year	Mo.	%	Mo.	%	Mo.	Total days
1965	Apr.	13.0	Nov.	39.8	June-Aug.	59
1966	Mar.	15.0	July	40.0	May-June	60
1967	Apr.	18.2	June	43.5	Mar.-May	69
Mean		15.4		41.1		63

[1] Data illustrated in Figure 8; from Lasker and Smith (1977).

This analysis indicates that the annual spring bloom might regulate the reproductive potential of the northern anchovy population. This effect may have a 1-yr lag because fat accumulated in the late spring and summer would presumably be used to support reproduction the following year because most spawning occurs in February through April. On the other hand, if 20 spawnings occur, about one-third of them would have to be supported from energy gained during the current year. Thus, production of plankton might have an effect on egg production late in the spawning season, but the major effect of the spring bloom on reproduction may occur the following year.

ENERGY BUDGET FOR FEMALE GROWTH AND REPRODUCTION

In this section we calculate an annual energy budget for reproduction and growth in female northern anchovy based on relationships established in past sections and in the laboratory ration study outlined below. Food ration (R) may be partitioned into energy losses of metabolism (Q), excretion (X), digestive losses (I), reproductive costs (S), gains in growth (N) and fat stores (F) where

$$R = Q + X + I + S + N + F. \tag{7}$$

We do not estimate Q, X, or I, but rather calculate for laboratory females the gross conversion efficiency (C) where

$$C = \frac{S + N + F}{R}. \tag{8}$$

Variables N and F were calculated by subtracting weight and fat content of females determined at the beginning of the experiment from that determined at the end (Table 6); reproductive cost S was simply the increase in weight of the ovary since the fish did not spawn during the experiment; and R was calculated using Equation (5).

The coefficient C was used to estimate ration for natural populations using

$$R = \frac{S + N}{C}. \tag{9}$$

TABLE 6.—Calories gained per day and daily ration of two groups of northern anchovy fed Oregon Moist Trout Pellets.

	Standard length (mm)		Fat-free dry weight (without ovary) (g)		Fat in body (without ovary) (g)		Ovary dry weight (including fat) (g)	
Item	Beginning	End	Beginning	End	Beginning	End	Beginning	End
			Group 2					
Mean	108	120	2.38	3.27	1.17	2.66	0.14	0.38
SE of mean	.86	1.04	.09	.12	.30	.18	.02	.02
Number of fish	21	19	21	19	21	19	21	21
			Group 3					
Mean	106	122	2.16	3.30	.70	2.54	.04	.38
SE of mean	1.51	1.31	.10	.08	.03	.11	.02	.03
Number of fish	24	18	24	18	24	18	24	18

			Calories gained per day[1]			
Group	Duration of experiment (d)	Daily ration[2] (cal)	Body (less ovary) (fat free)	Fat	Ovary (including fat)	Total
2	69	2,238	53	199	19.8	271
3	78	2,245	60	218	24.9	303
Mean	73.5	2,241	56	208	22.4	287
Percentage of ration			2.5	9.2	1.0	12.8

[1] Caloric values in Table 2

[2] Method of calculation of ration outlined in methods

Fat stores (F) are included in calculation of C in the laboratory work (Equation (8)) but not in the ration for natural populations (Equation (9)) because on an annual basis it is assumed to be subsumed in the annual cost of reproduction. The caloric value used for growth was set at the minimum fat content of the year (15.4% of the dry weight) using values in Table 2 and Equation (1).

Laboratory Growth Efficiency

Northern anchovy (groups 2 and 3) maintained in the laboratory grew much faster than those in the sea. The growth in length was about four times that estimated for wild northern anchovy by Spratt (1975) but was seven times faster when Spratt's data were converted to wet weight using the length-weight conversion for females of Collins (1969) (solid line, Figure 9). Thus, the average ration consumed by northern anchovy in the laboratory, 2,241 cal/d (about 124 cal/g fish wet weight per d) is probably much larger than the one consumed in the sea. On a wet weight basis, the laboratory ration (4.5% of fish wet weight/d) is deceptively low because the pelleted food had a much lower water content (35%) than natural foods (85%). A caloric equivalent ration of natural foods (copepods) would be about 16% of the wet weight/d.

Spawning did not begin during the experiment, hence the proportion of the daily ration incorporated into the ovaries (0.8%) was a function of only maturation of the ovary (Table 6). The median of the mean major axis of the eggs in the most advanced batch in the ovary increased from 0.55 to 0.63 mm in group 2 and from <0.25 to 0.63 mm for group 3. Most of the caloric gain was in fat; the percentage of the dry weight that contained fat increased from 32.6 to 44.2% in group 2 and from 24.5 to 43.2% in group 3 and accounted for about 9.2% of the daily ration. The caloric conversion efficiency for the total gain of calories in the body (including ovary and fat) was 12.8%. We calculated from data of Takahashi and Hatanaka (1960)

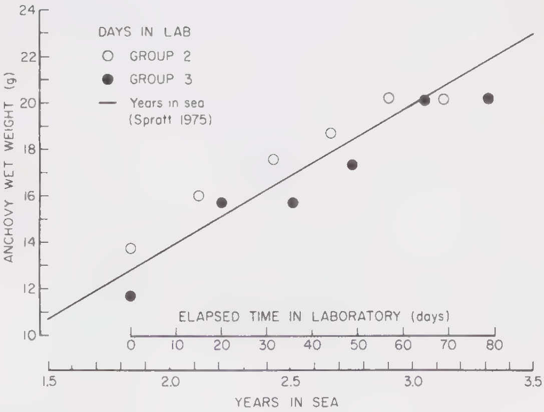

FIGURE 9.—Growth in days of two groups of northern anchovy in the laboratory (dots and circles) compared with the growth over years of northern anchovy in the sea (solid line). Growth in the laboratory is plotted using upper scale (elapsed time days), and growth in sea (solid line, from Spratt 1975; Collins 1969) is plotted on lower scale (years); and ratio between scales is about 1:7. Each point is mean weight for 8-12 fish. Laboratory fish were fed a pelleted trout ration which was the caloric equivalent in natural foods of about 16% of the fish wet weight per day.

that the Japanese anchovy, *Engraulis japonicus*, fed *Euphausia pacifica* in the laboratory, had a gross growth efficiency (in calories) of 11.9%, which is similar to our estimate of 12.8% for *E. mordax*.

Energy Budget

Growth of northern anchovy in the sea from age 1 to 2 yr is equivalent to a gain of 6.2 × 10^3 cal, and the energy cost of 20 spawnings for a 1-yr-old female is about 10 × 10^3 cal (documentation given in Table 7). Assuming that the caloric conversion efficiency for northern anchovy in the sea is the same as in the laboratory (12.8%), 1-yr-old females (mean weight 10.3 g) consume annually about 127 × 10^3 cal of which 8% would be used for reproduction and 5% for growth. This implies a daily rate of consumption in the sea of 348 cal/d, or, on a wet weight basis, about 4% body wet weight/d in copepods (copepods = 5,252 cal/g dry weight, Laurence (1976); water content of *Calanus* = 84.7%, Lovegrove (1966)). Sirotenko and Danilevskiy (1977) estimated from stomach content analysis that the Black Sea anchovy, *E. encrasicholus*, consumed 1.5-3.7% of their body weight/d; Mikhman and Tomanovich (1977) estimated from field captured specimens that *E. encrasicholus* consumed 1.4-3.0% of their body weight/d when they fed upon phytoplankton, 3.4% when they ate zooplankton, and 9.3% when they ate benthic animals. Our estimate of 4-5% body weight/d for females 1-3 yr old is within the range of these values.

DISCUSSION

Spawning Frequency

Northern anchovy females matured eggs in the laboratory at the rate required for weekly spawning, thus supporting the conclusions of Hunter and Goldberg (1980) and Hunter and Macewicz (1980). Our estimates of reproductive effort (egg calories/ration calories) of 8-11% (Table 7) seem reasonable, thereby supporting our estimate of 20 spawnings/female per year. Our calculations indicate that this effort could be sustained by a daily ration of natural foods of 4-5% of the fish wet weight/d which is similar to the natural ration of *E. encrasicholus* (Sirotenko and Danilevskiy 1977; Mikhman and Tomanovich 1977). Few estimates of reproductive effort exist for fishes. Lasker (1970) estimated that the cost of reproduction in Pacific sardine, *Sardinops sagax*, was about 1% of the total annual caloric requirement. He assumed the caloric equivalent of the ovary is spawned per year, which now seems an underestimate. Constantz (1976) estimated that reproductive effort ranged from 4 to 15% in two populations of *Poeciliopsis occidentalis*. Hirshfield (1977) found in laboratory studies that reproductive effort was related in a complex fashion to temperature and ration in medaka, *Oryzias latipes*; he estimated reproductive effort ranged from 10 to 18% in two natural Japanese populations. We conclude that 20 spawnings/yr is a reasonable estimate of the number of spawnings produced by females in the northern anchovy central subpopulation. The fact that two-thirds of the cost could be supported by the average annual decline in fat stores supports this conclusion.

An implication of this study is that egg maturation and vitellogenesis are continuous during peak spawning months. Evidence for this includes: the large fraction of the females in the population spawning per day during peak spawning months (10-16%); the presence of the caloric equivalent of only one or two spawning batches in the ovary at any time; the inverse relation between the abundance of egg sizes in the ovary and oocyte maturation rate; and the continuation of egg maturation until the last batch of eggs is spawned. Although maturation and vitellogenesis probably continue for extended periods, the rates probably vary. The seasonal decline in the fraction of females in the

TABLE 7.—Annual energy budget for female northern anchovy.

Age (yr) Beginning-end	SL[1] (mm) Beginning-end	Wet weight[2] (g) Beginning-end	Annual energy budget (thousands of calories)			Percentage of ration	
			Growth[3]	Reproduction[4]	Ration[5]	Growth	Reproduction
1-2	93-112	7.33-13.25	6.24	10.00	127	5	8
2-3	112-126	13.25-19.33	6.38	21.0	214	3	10
3-4	126-136	19.33-24.69	5.60	34.3	312	2	11

[1] From Spratt (1975)

[2] From Equations (1) and (2) where 15.4% of dry weight = fat.

[3] Gain in calories assuming 15.4% of dry weight = fat; caloric values in Table 2.

[4] Caloric content of 20 spawning batches; batch size calculated for mean female wet weight over the year (method illustrated in Table 4).

[5] Reproduction calories + growth calories/0.128, where 0.128 is growth conversion efficiency determined in laboratory (Table 6).

population spawning per day indicates that either the interval between spawnings in individual females increases in the latter part of the spawning season, or that an increasing number of females cease spawning as the season progresses, or a combination of both events. Rates of egg maturation and vitellogenesis probably also vary within a single maturation-spawning cycle. The caloric content of a northern anchovy ovary about doubles over the interval between spawnings (7-10 d in peak spawning months), indicating a rapid rate of vitellogenesis after spawning. In *Brachydanio rerio*, which spawns at 5-d intervals, a marked increase in gonadotropic activity occurs in the pituitary immediately after spawning (Lambert and van Oordt 1974), followed 1-2 d later by histological signs of an increase in lipoprotein production in the liver correlated with an increase in vitellogenesis (Peute et al. 1978). Similar processes may occur in northern anchovy, causing cyclic changes in the rates of vitellogenesis and egg maturation within the interval between spawnings.

Our estimate of 20 spawnings/yr is much higher than the number of spawnings estimated for many other pelagic spawning clupeoid fishes or for pelagic spawners in general. Multiple spawning fishes such as pilchards, sardines, anchovies, jack mackerels, and mackerels are often believed to produce one to three and possibly more spawning batches per year. These conclusions are based on the fact that frequently two modes of yolked eggs and sometimes three (in females with hydrated eggs) are observed in frequency distributions of ovarian egg sizes. Eggs are distributed in the same way in the northern anchovy (MacGregor 1968; Hunter and Goldberg 1980), but as present studies indicate, estimates of one to three spawnings would be in error by a factor of about 10. Thus, comparisons of annual fecundity among pelagic spawning clupeoids are meaningless at present, and spawning biomass estimated from egg and larval surveys may be in error because the total fecundity is inaccurate. Because of this it is essential that spawning frequency be estimated for additional species.

The best approach, at present, is the histological technique of Hunter and Goldberg (1980), but counts of the number of females with hydrated eggs could be used if histological techniques are impractical. Females with hydrated eggs are often rare in collections of clupeoid females taken during the spawning season (Higham and Nicholson 1964; Leary et al. 1975). Females with hydrated eggs may be available for sampling for only a short period of each day because hydration is rapid and spawning soon follows hydration. In northern anchovy, hydration is completed in about 12 h, but the earliest stage may not be evident without histological examination. In tropical species the time available for sampling females with hydrated eggs may be even less because of elevated temperature. The daily pattern of hydration and spawning must be known to use hydrated eggs as a measure of spawning frequency. It may also require sampling of fish in the day, because many pelagic spawners such as the northern anchovy begin spawning at sunset (Blaxter and Holliday 1963; Leary et al. 1975; Hunter and Macewicz 1980).

Variation in Egg Production and Reproductive Effort

Annual egg production and/or reproductive effort in northern anchovy populations can be modulated by changes in batch fecundity, annual number of spawnings, female size at first maturity, egg size, and egg cannibalism. Some evidence exists for each of these mechanisms in northern anchovy populations; we consider the evidence below.

Batch fecundity was relatively constant over 1978-79 (Hunter and Macewicz 1980) and was similar to that of laboratory specimens fed a large food ration. On the other hand, MacGregor (1968) estimated a somewhat higher fecundity for the central stock in the 1950's than Hunter and Macewicz (1980) did for the 1970's, and Laroche and Richardson (1981) found that batch fecundity of the northern subpopulation (Oregon coast) was much higher than all estimates for the central stock. Batch fecundity certainly differs between central and northern subpopulations, and it seems possible that it may have varied within the central stock over the last decades. Nevertheless, batch fecundity within a subpopulation may be a relatively more stable reproductive characteristic than other reproductive traits.

Weight at first maturity and age structure of the spawning population have a major effect on egg production, since batch size in northern anchovy increases exponentially with weight. Clark and Phillips (1952) concluded for females taken in 1946-52 from the central subpopulation that 50% of northern anchovy reach maturity at 130 mm SL whereas Hunter and Macewicz (1980) estimated for 1979 that 50% of females of 96 mm SL were mature. Laroche and Richardson (1981) reported that only 31% of females 85-100 mm SL from the northern stock were mature. Thus, size at sexual maturity varies between subpopulations and may have varied within the central subpopulation over the last decade.

The relatively short 2-mo spawning season of the northern subpopulation of northern anchovy (perhaps 4 to 8 spawnings, Hunter and Macewicz 1980) compared with the central subpopulation (20 spawnings) is evidence of the great plasticity in the annual number of spawnings. Plasticity in the number of spawnings of the central stock is also indicated by the dynamics of the central population over the last decades. Smith (1972) pointed out that the decline of the Pacific sardine population was accompanied by an increase in the duration of the northern anchovy spawning period. Before the Pacific sardine decline, most northern anchovy spawning occurred in the winter quarter, whereas now larval production in both quarters is about equal. This increase in the duration of the peak period of spawning indicates that the annual number of spawning batches produced by northern anchovy has changed significantly since the demise of the Pacific sardine population. Food made available by the collapse of the Pacific sardine population may have been used by the northern anchovy population to increase the number of spawning batches produced annually. The fact that these additional spawnings occurred during the period Pacific sardine normally spawned may have had an important effect on the Pacific sardine population.

The annual seasonal decline in egg size in northern anchovy population (central stock) resembles that reported for other clupeoid fishes (Blaxter 1969; Ciechomski 1973; Le Clus 1979). Production of smaller eggs late in the season may be an energy-sparing mechanism whereby fecundity is maintained constant but at a lower reproductive effort. This could represent a 20% savings in reproductive costs in northern anchovy. Bagenal (1973) concluded in his review of the literature that it seems likely a negative correlation exists between fecundity and egg size. Several other mechanisms are possible; egg size may increase with female age (Hirshfield 1977), and the seasonal change could be caused by seasonal changes in the age structure of the spawners. In this case smaller eggs may compensate for the energy cost of faster growth in young fish. Alternatively, egg size may decline in females as ration increases during the spring and summer. Bagenal (1969) found that higher ration in brown trout resulted in more and smaller eggs. On the other hand, Hislop et al. (1978) found that the dry weight of eggs produced by haddock in the laboratory declined with successive spawnings and that the dry weight of eggs tended to be lower in females fed a lower ration. In northern anchovy, there may be a change in the partitioning of energy between growth and reproduction during late spring and summer when the potential for growth is higher, and this could result in the production of smaller eggs. As egg size alters the survival potential of the larva (Blaxter and Hempel 1963), any of these mechanisms could have important consequences because it could alter the relative contribution to recruitment of spawn produced in the latter part of the spawning season.

Egg cannibalism may also be an important factor regulating the effective egg production, as intensity of cannibalism could change with population size. Hunter and Kimbrell (1981) concluded that ingestion of eggs by northern anchovy could account for 17% of the daily egg production during peak spawning months.

This discussion indicates that egg production and reproductive effort of northern anchovy populations probably changes in a complex manner in relation to food, growth, temperature, population size, and age structure. All the reproductive parameters we have discussed may vary to some degree over years, between subpopulations, or within a season.

Studies of the reproductive energetics of northern anchovy populations will eventually require consideration of males as well as females. We know little about males at present. Our laboratory data indicated that males consume slightly less food than females, but no difference existed when consumption was expressed on a unit weight basis. Growth curves for male and female northern anchovy (Collins 1969) indicate that females are slightly longer than males of the same age, but the difference is small (about a 2% difference in length) and probably not statistically significant. Other than this small difference in size, no obvious sexual dimorphic characters exist. Schools have highly biased sex ratios (Klingbeil 1978), and males predominate in actively spawning schools (Hunter and Goldberg 1980). This suggests that males may remain reproductively active for longer periods within the spawning season and may not have as well defined spawning cycles as do females. These differences are small relative to the overall great similarity between the sexes.

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8122

Feeding Ecology and Predation of Marine Fish Larvae

John R. Hunter

The objective of my three lectures in this series is to describe some of the behavioral and physiological characteristics of marine fish larvae that affect their survival and growth. The two major sources of larval mortality are probably starvation and predation. The first two lectures deal with feeding ecology of marine fish larvae; I point out differences in life history strategy and how such differences affect the ability of larvae to avoid starvation. These two lectures came from a review I had written in 1977 (Hunter, 1980), and that review is reproduced here with only minor changes. In my last lecture I discuss the problem of predation on eggs and larvae and make some general conclusions. In all lectures, I depend on my research and that of colleagues at the Southwest Fisheries Center in La Jolla, California.

Feeding Ecology

Parental Effects

Egg Size, Yolk Quantity, and Starvation

The size of a larva at the time of first feeding and the amount of time available to find food before onset of irreversible starvation are largely determined by the maternal influence of egg size and by water temperature. Shirota (1970) found that the length in millimeters of 40 species of marine and freshwater larvae at onset of feeding was related to egg diameter in millimeters by the simple relationship $L = 4D$. Large size at onset of feeding is an advantage because larger larvae are able to swim faster and search a greater volume of water for food.

As shown in Table 1, larvae from large eggs generally have more time to find food before the onset of irreversible starvation, because yolk persists for a longer period after feeding begins and the larvae have greater reserves in their body which can be used in metabolism (Blaxter and Hempel, 1963). Larvae from small pelagic eggs are capable of existing for about 1–2 days after yolk absorption before onset of irreversible starvation, whereas larvae from large eggs such as herring and plaice are able to exist for 6 days after yolk absorption, and in grunion larvae starvation is still reversible after 16 days (May, 1971). The ability to withstand starvation increases steadily from this point. At the beginning of metamorphosis, herring can withstand 15 days, plaice 23 days (Blaxter and Ehrlich, 1974), anchovy 14 days, and Pacific mackerel larvae 5 days (Hunter, 1976b; Hunter and Kimbrell, 1980a). These differences reflect in part differences in activity; plaice are less active than herring at this time (Blaxter and Ehrlich, 1974) and anchovy less than mackerel. Differences between older fishes reared in the laboratory must be considered only in a relative sense because of the striking differences in condition between reared and wild animals (Blaxter, 1975).

The duration of egg incubation, although strongly affected by temperature, is also influenced by egg size. Ware (1975) found the relationship between the incubation time (I; days) at the water temperature for peak spawning and egg diameter (D; mm) for 14 species of Northwest Atlantic fishes was $D = 0.101 I + 0.67$. Similarly, the duration of the yolk sac stage is also affected by egg size (Blaxter and Hempel, 1963). Thus, larger eggs improve the survival capabilities of a larva at the onset of feeding, but at the

Table 1. Vulnerability to starvation of eight marine fish larvae at the time of first feeding.

		Size at hatch		Yolk absorption	Days to point of no return[a] relative to:		
Species	Temp. °C	Length mm	Dry weight μg	Period days	Hatch	Yolk absorption	Onset of feeding
GRUNION[c] *Leuresthes tenuis*	20	9.0	362	4	12 +[b]	8 +[b]	12 +[b]
CLYDE HERRING[d] *Clupea harengus*	7–8	8.2	189	8	25	6	22
HADDOCK[e] *Melanogrammus aeglefinus*	7	3.5	—	6–7	6	0–1	—
PACIFIC MACKEREL[f] *Scomber japonicus*	19	3.1	40	3	4.0	1.0	1.6
NORTHERN ANCHOVY[g] *Engraulis mordax*	16.5	2.9	21	4	7.7	1.5	2.5
BAY ANCHOVY[h] *Anchoa mitchilli*	24	2.5	18	1.7	3.1	1.4	1.7
SEA BREAM[h] *Archosargus rhomboidalis*	22	2.3	28	2.2	3.4	1.2	1.7
LINED SOLE[h] *Archirus lineatus*	24	1.9	22	3.3	3.8	0.5	1.3

[a] Time of irreversible starvation (Blaxter & Hempel, 1963).

[b] 50% mortality from starvation, not a point of no return, because all survivors able to survive if fed.

[c] May (1971).

[d] Blaxter & Hempel (1963); Blaxter & Ehrlich (1974).

[e] Laurence (1974); Laurence & Rogers (1976).

[f] Hunter & Kimbrell (1980).

[g] Lasker et al. (1970); Hunter (unpubl. data).

[h] Houde (1974); Houde (1978).

cost of decreasing fecundity and increasing the duration of stages most vulnerable to predation.

The optimum egg size must strike a balance between numbers and the risks of starvation and predation. At lower temperatures, where incubation periods are longer, the advantage generally falls to larger eggs, whereas the reverse appears to be true at higher temperatures (Ware, 1975). Fine adjustments in these tactics appear to exist within a species to meet seasonal and regional differences in environment. Egg size varies significantly among spawning groups of herring (Blaxter and Hempel, 1963) and is known to vary seasonally in many species, with the largest eggs produced in the spring at the coolest temperatures and egg size declining as the season progresses (Bagenal, 1971; Ware, 1975).

The estimation of days to irreversible starvation has generally been made from the time of complete yolk absorption, but the time from onset of feeding provides more insight to survival strategy, as most larvae begin to feed before the yolk is completely exhausted. Herring larvae have a prolonged period in which they are capable of feeding but still have yolk (Table 1). The thermal optimum in efficiency of yolk utilization is another possible larval adaptation to specific environmental conditions. Sea bream larvae ret more yolk at the onset of feeding at 26°C than at other temperatures and tl have more yolk to sustain them if food is not present (Houde, 1974). Pla larvae have a sharply defined thermal optimum in yolk utilization efficie between 6.5°C and 8°C, which if realized could produce larvae 10 perc larger at the time of first feeding (Ryland and Nichols, 1967).

Spawning Tactics

Eggs of pelagic spawners are often distributed in extremely patchy p terns; 37% of Pacific sardine eggs taken in the years from 1951 to 1959 curred in only 0.6% of the samples (Smith, 1973). Helfrich and Allen (19 found the density of mullet eggs, *Crenimugil crenilabis,* to be 17 eggs/l at surface after about one or two seconds of intensive spawning. A high den of northern anchovy eggs taken in a neuston net was 31 eggs/l, correspond to a density of 46,000 eggs per 10 square meters of sea surface, which is in upper 5% of all samples of anchovy eggs collected with nylon nets (unp lished data, NMFS, Southwest Fisheries Center, La Jolla). Other high egg d sities include 31,000 eggs per 10 square meters for Pacific sardine (Sm 1973) and 9,000 eggs per 10 square meters for Atlantic mackerel (Se 1943).

The eggs in such patches gradually disperse; dispersion is more rapi the perimeter of the patch, resulting in a denser centrum surrounded b less concentrated corona. The horizontal mean distance between neighb ing eggs increases in a patch from one to two centimeters at spawnin 15–20 cm in most several-day-old sardine eggs (Smith, 1973). In north anchovy, dispersion of larvae as measured by the negative binomial K (Ll 1967) continues from hatching until the larvae attain a length of abou mm, at which time they reach their most dispersed stage and contagior creases thereafter (J. Zweifel, unpublished data, NMFS, Southwest Fishe Center, La Jolla). This change from decreasing to increasing contagion c cides with the time anchovy begin nightly migrations to the sea surface t their swim bladders (Hunter and Sanchez, 1976) and is close to the ons schooling, which begins at about 13 mm. Vertical migration may set stage for schooling by concentrating larvae near the surface at night and increasing the frequency of social contacts.

Dispersion of larvae could progress to the point where it might influ onset of schooling or delay formation of schools of viable size. *Menidia* la reared in isolation took more time to form a school when brought toge than socially reared larvae, and the length of the delay was proportion the period of isolation (Shaw, 1961). Breder and Halpern (1946) showed *Brachydanio rerio* larvae reared from the egg in isolation were quite hes to join a school. Thus, onset of schooling could be retarded if larvae are persed to the point where social contacts are infrequent.

Intraspecific competition and cannibalism also may be affected b tial spawn density and dispersion rates. Houde (1975) found that growt survival of sea bream decreased rapidly when stocking density exceeded 8 eggs/l at food levels of 1500–3000 microcopepods/l. Food concentrations of 100 microcopepods/l did not sustain sea bream larvae except at stock densities of 2 eggs/l. Bay anchovy larvae *(Anchoa mitchilli)* seem to be much less affected by stock density (Houde, 1975, 1977). Sibling cannibalism is common in rearing larvae of large piscivorous fishes such as the scombroids (Mayo, 1973), but is unreported and presumably rare in clupeoid fishes. Thus, larger and more active larvae seem to be more cannibalistic and competitive for food and possibly better able to find schooling companions because of faster swimming speeds. Formation of dense patches of eggs and slow dispersion rates may favor clupeoid larvae, but lower egg densities may be more favorable to the more active larvae.

Swimming Behavior

Swimming during the yolk-sac stage consists of bouts of continuous, very energetic swimming followed by relatively long periods of rest. This behavior appears to be common in many small marine yolk-sac larvae but has been described in detail for only the northern anchovy (Hunter, 1972; Weihs, 1980). This mode of swimming in anchovy larvae is energetically advantageous for yolk-sac anchovy larvae because water viscosity is the dominant factor when larvae are in this stage (low Reynolds number). When larvae reach 5 mm, the Reynolds number is sufficiently high that beat and glide swimming becomes the more economical mode (Weihs, 1980).

After conclusion of the yolk-sac period, the cruising speed of larvae becomes of major importance in their feeding ecology, because it affects the frequency that larvae encounter prey and also accounts for the greatest metabolic expenditure. Swimming of larvae in this period may also differ somewhat from adults, due in part to the lack of mechanical support of the caudal fin and to the low Reynolds number (Weihs, 1980). Tail-beat amplitude and tail-beat frequency are continuously modulated in northern anchovy larvae (Hunter, 1972) and Pacific mackerel larvae (Hunter and Kimbrell, 1980a), whereas in adult fishes amplitude is modulated less frequently, except during accelerations (Hunter and Zweifel, 1971). Because tail-beat frequency is inversely proportional to length in fishes (Bainbridge, 1958; Hunter and Zweifel, 1971), the frequency in early larval stages can be quite high, reaching 50 beats per second in 4–5 mm anchovy and Pacific mackerel larvae. At their cruising speed, anchovy larvae use a beat and glide mode of swimming similar to that of adults. This mode of swimming is slow and thereby reduces the volume of water that can be searched, but it has a high metabolic efficiency—25% in a 14 mm larva (Vlymen, 1974).

Temperature can have a major effect on activity or cruising speed. Two effects of temperature on activity are illustrated in Figure 1 for northern anchovy reared to age 12 days at various temperatures on a diet of *Gymnodinium splendens*. Temperature affected the timing of the transition from the

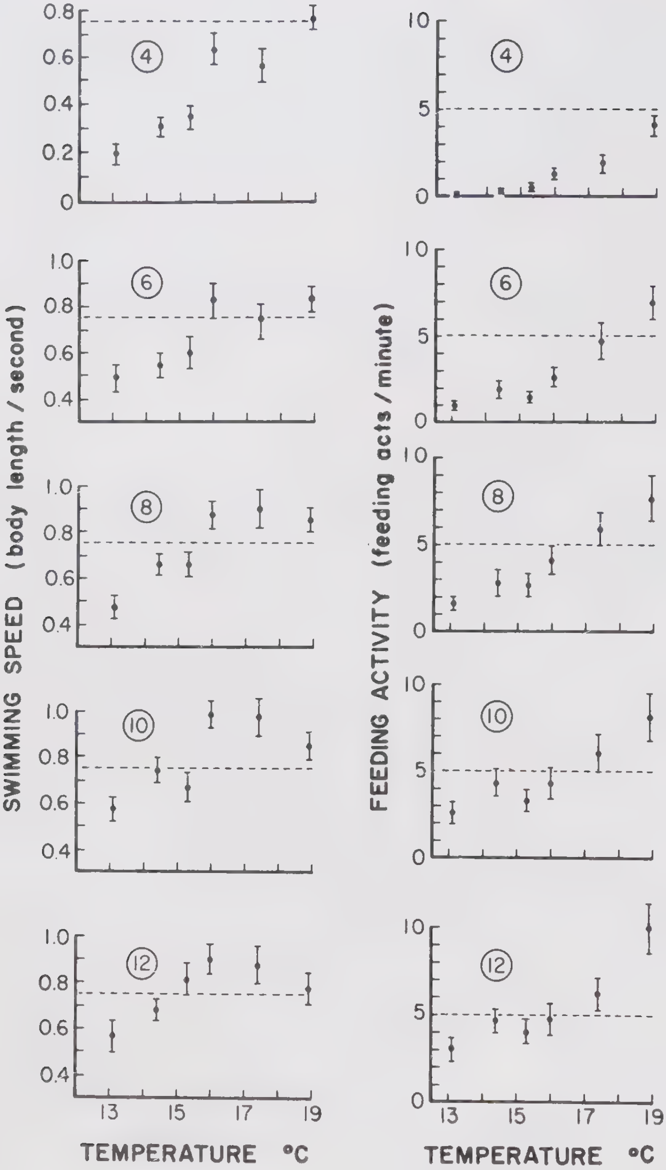

Figure 1. Effect of temperature on swimming speed and feeding rate of northern anchovy fed *Gymnodinium splendens* (mean density 400 cells/ml). Points are means, bars are 2 × standard error of mean, panel numbers are larval age in days, and dashed line is a visual reference. Data based on direct visual observation of larvae for 5 min. intervals. Each point average of value for 15 fish in two or more rearing groups.

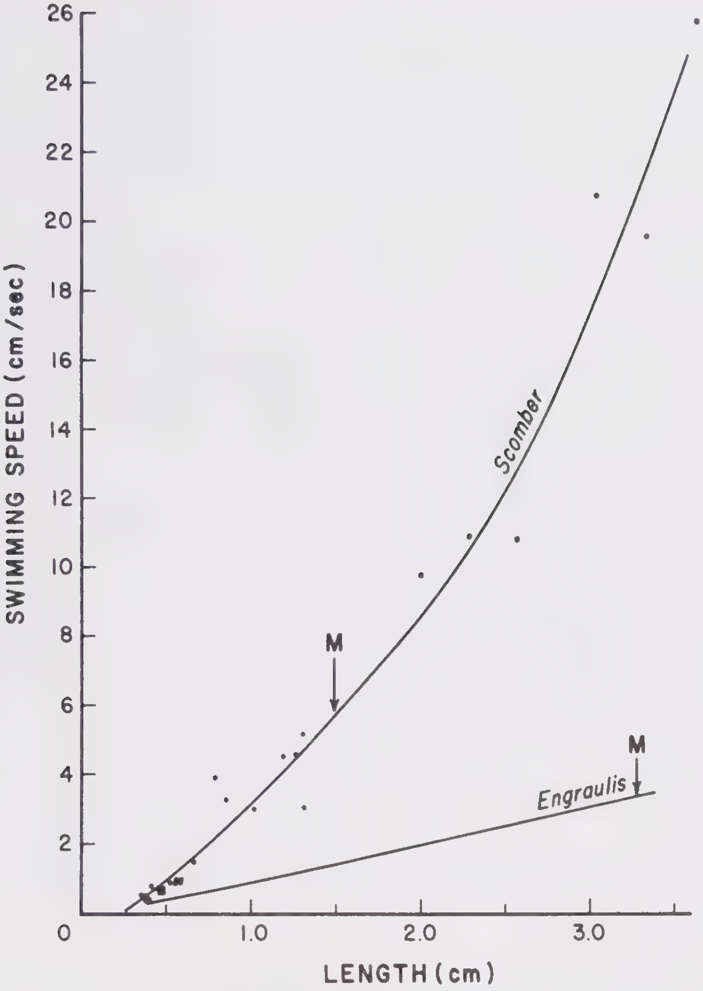

Figure 2. Swimming speed of Pacific mackerel, *Scomber japonicus*, larvae and juveniles at 19°C; points are means for five or more observations; curve fit by eye; and swimming speed of northern anchovy larvae, *Engraulis mordax*, at 17°C–18°C from Hunter (1972). Speeds are total distance covered including time spent in rest and feeding, and M indicates fish length at metamorphosis.

inactive yolk-sac stage to the active feeding stage as well as having a direct effect on activity of older larvae. At age 4 days, negligible feeding activity occurred in larvae at 15°C or lower, and the speed-temperature relation was a function of developmental rate. At ages 8–12 days, all larvae were past this transition. A direct effect of temperature on activity is evident in the figure.

Cruising speeds increase markedly over larval life more or less in proportion to length. Blaxter and Staines (1971) observed that the cruising speed of herring larvae increased from 20 cm/min at the end of yolk-sac stage to 80 cm/min 8 weeks later; in pilchard (*Sardina pilchardus*) speed increased from 10 to 30 cm/min in 3 weeks; in plaice from 10 to 60 cm/min over 7 weeks; and in sole (*Solea solea*) from 5 to 40 cm/min over 7 weeks. They also noted that cruising speeds of flatfish, sole, and plaice dropped by 90% at metamorphosis. Similarly, oxygen consumption of winter flounder, *Pseudopleuronectes americanus*, was shown by Laurence (1975) to decline sharply at metamorphosis.

Specific comparisons in activity or swimming speed from the literature are difficult to make because of differences in temperature, methodology, and lack of data on larval size. Data collected in my laboratory on anchovy and mackerel show that anchovy larvae swim more slowly than mackerel larvae at all stages of development (Fig. 2). Such a striking specific difference in cruising speed is diagnostic of major differences in life history tactics because it implies marked differences in searching abilities and metabolic requirements. For example, at 18°C, anchovy larvae consume 4.5 μl 0_2/mg dry wt/hr, whereas mackerel consume 6.1 μl 0_2/mg dry wt/hr (Hunter, 1972; Hunter and Kimbrell, 1980a). The actual difference in metabolic rate between these species is probably greater because the larvae were confined in small Warburg flasks which probably reduced the activity.

Blaxter (1969) concluded from his review that cruising speeds of larval fishes are on the order of 2–3 body lengths/sec and burst speeds (speeds that can be maintained for a few seconds) are on the order of 10 body lengths/sec. The cruising speed of anchovy is close to 1 body length/sec, and in mackerel it increases from 2 to 3 during the larval stage. Thus, these two speeds approach the upper and lower limits of the general range of cruising speeds.

Feeding Behavior

Prey Perception and Recognition

Marine fish larvae are visual feeders. All those studied so far—plaice, herring, and anchovy—lack rods and retinomotor pigment migration during the first weeks or months of life (Blaxter, 1968a, 1968b; O'Connell, 1981). That feeding is confined to daylight hours is also indicated by stomach content analysis in other species (Arthur, 1976).

To be perceived, a prey must be relatively near; first-feeding herring larvae react to prey at 0.7–1.0 body length L (Rosenthal and Hempel, 1970) or 0.4L (Blaxter and Staines, 1971), plaice at 0.5L, and pilchard at 0.2L (Blaxter and Staines, 1971). Ninety-five percent of the prey reacted to by northern anchovy were within 0.4L of the axis of progression (Hunter, 1972).

It would be unreasonable to attach much importance to differences between species among these values. The factors controlling perceptive ranges in larval fishes have not been studied, and size of prey was not isolated as a variable. In adult planktivorous fishes, perceptive distances appear to be a linear function of prey size (Confer and Blades, 1975). If perceptive distances increase with prey size in larvae, this would certainly increase the effective searching volume of larvae specializing in such prey. In all these studies, the authors point out that perceptive ranges increase as larvae grow. Rosenthal and Hempel (1970) concluded that perceptive ranges in herring larvae also change with activity level, being greater during slow meandering swimming and shorter during faster swimming. They also state that herring larvae do not perceive prey which are beneath the plane of the horizontal axis of the body, but this does not appear to be the case for nothern anchovy larvae (Hunter, 1972).

The stimuli eliciting prey capture have not been studied in larval fishes, but in adult fishes prey size is usually the strongest factor, with movement seeming to direct attention of the fish toward the prey (Kislalioglu and Gibson, 1976a). Almost all predators which are believed to depend upon prey movement are able to detect prey even when it is motionless (Curio, 1976). The frequent occurrence of copepod eggs and other nonmotile foods in the stomachs of field-caught larvae and *Artemia* eggs and other nonmotile foods in laboratory-reared larvae (May, 1970) clearly shows that movement is not essential in many species. Prey size selection so dominates selection patterns in larval fish that it is difficult to evaluate the role of other prey characteristics such as spines and other protective structures, color, or avoidance behavior. Bowers and Williamson (1951) concluded that some copepods with spiny appendages, such as *Acartia*, occur in the stomachs of herring larvae less frequently than would be expected from their abundance in the plankton, and Arthur (1976) suggested that jack mackerel may select the more brightly colored copepods such as *Microsetella*, which occur in their stomachs in greater abundance than seen in the plankton. It would be of considerable interest to study such characteristics under controlled laboratory conditions from the standpoint of both larval feeding ecology and copepod evolution.

Motor Patterns

Upon sighting a prey, a clupeoid larva forms a sinuous posture and advances toward the prey by sculling the pectoral fins and undulating the finfold while maintaining the body in the S-posture. When the prey is a short distance from the snout, the larva opens its mouth, straightens its body to drive forward, and engulfs the prey (Breder and Krumholz, 1943; Rosenthal and Hempel, 1970; Hunter, 1972). Larvae of plaice, *Pleuronectes platessa* (Riley, 1966), and northern sennet, *Sphyraena borealis* (Houde, 1972), and other fishes are also reported to form a sinuous feeding posture, but the behavior has been studied in detail only for clupeoids and for the freshwater coregonid larvae, *Coregonus wartmanni* (Braum, 1967), and quite possibly differences exist among species.

Mackerel larvae, *Scomber japonicus*, feed in a manner more typical of the attack of many adult fishes. Upon sighting a prey, the larva advances toward the prey, stops, draws back the tail, and holds it in a slightly recurved high amplitude position (the C-start position of Webb, 1978). The rest of the body is straight; feeding is accomplished by opening the mouth and driving the tail posteriorly. Presumably many other larvae of similar robust body form feed in this way.

Anchovy larvae often form and reform the S-posture while maintaining their orientation to a moving prey; but my observations indicate that, once the strike is made, anchovy larvae rarely strike again at the same prey. Mackerel larvae, on the other hand, frequently strike two or more times at the same prey if the preceding strike was unsuccessful. Mackerel larvae often reposition for the second strike by moving backward; anchovy and other clupeoid fishes do not appear to have this maneuverability (Blaxter and Staines, 1971). Large prey are more difficult to capture and are less abundant in the sea; consequently, persistence in a feeding attack as exhibited by mackerel may be an essential characteristic of a species whose strategy depends on larger prey.

Webb (Paul Webb, University of Michigan, Ann Arbor, unpublished data) described in detail the starting postures of feeding pike and largemouth bass. He concluded that pike, which use an S-start as do anchovy larvae, are less persistent in the attack and strike at higher speeds and at shorter range than do bass, which use a C-start. The parallels between his observations and ours on mackerel and anchovy larvae seem obvious.

The time spent poised in a striking posture in anchovy larvae is much longer at the time of first feeding than in later larval life, and gradually the strike becomes integrated with swimming movements; the duration of complete feeding acts declines from 1.5–2.0 seconds to about 0.6 seconds when larvae reach 17 mm, and relative speed of the strike also declines (Hunter, 1972). The poised stereotyped striking posture (C- or S-starting position) seems to be a common tendency in young larvae and becomes integrated into swimming movements as the larva grows, and suggests that it may be an adaptation to feeding on relatively large and fast prey. As will be shown subsequently, young anchovy larvae feed on much larger prey relative to their size than do older larvae.

Handling times are negligible when copepods and other small zooplankton are prey because the prey are engulfed by the mouth instantaneously. Piscivorous fish larvae manipulate their prey, and consequently handling times increase with prey size as is the case for adult fishes (Kislalioglu and Gibson, 1976b). The appearance of piscivorous habits requires development of a new set of motor patterns associated with grasping prey and presence of a sufficient number of teeth to accomplish this end. Larvae of the northern sennet, *Sphyraena borealis*, usually seize other larvae crosswise and, by a successive series of head shakes, move the grasp to either the head or the tail. Then without losing grip, the prey is swallowed head or tail first (Houde, 1972). Houde observed that newly hatched fish larvae were eaten by sennets at age 10 days and were the preferred food of sennets 9 mm and longer. I observed the same behavior in the Pacific barracuda, *Sphyraena argentea*, feeding on siblings in a rearing tank. In this case, piscivorous feeding began at age 5 days when larvae were only 4.4 mm. Pacific mackerel larvae become piscivorous when they reach 10 mm. They also seize other larvae from the side, carry them crosswise in the mouth, periodically release the prey, and grasp it again until it dies. Then they release it and ingest it, usually head first.

Feeding Success

Feeding success of fish larvae is often low at the onset of feeding. Estimates for herring are 6% (Rosenthal and Hempel, 1970) and 2%–6% (Blaxter and Staines, 1971), for coregonid larvae 3%–5% (Braum, 1967), and for northern anchovy 10% (Hunter, 1972). Feeding success gradually increases, reaching 90% in about 3 weeks in anchovy (Hunter, 1972) and in about 7 weeks in herring (Blaxter and Staines, 1971). In contrast to these species, plaice larvae capture 32%–62% of prey attacked at the onset of feeding (Blaxter and Staines, 1971), and the relatively large larvae of *Belone belone* (12 mm) capture 60%–100%, depending on prey type (Rosenthal and Fonds, 1973).

Blaxter and Staines (1971) suggest that the initially high success of plaice larvae may be due to increased maneuverability of plaice relative to herring and to their ability to swim backwards. Feeding success of anchovy larvae dropped from 80% to 40% at age 17 days when the prey was changed from *Brachionus* to *Artemia* nauplii, but in 2 days their success increased to the former level (Hunter, 1972). Changes in mouth size or other developmental changes could not occur so rapidly, thus the difference appears to be attributable to experience.

Searching Behavior

Food density requirements have been estimated from behavioral search models of the basic form outlined by Ivlev (1960). These models in their simplest form require an estimate of ration, swimming speed, perceptive field, and feeding success, with many other parameters added as complexity increases. These models range in complexity from the simple models of Rosenthal and Hempel (1970), Blaxter and Staines (1971), and Hunter (1972), where only basic parameters are considered, to the increasingly complex models of Jones and Hall (1974) and—the most complex to date—Vlymen (1977). Vlymen's model is the only one that does not assume a random search pattern and that addresses the problem of a contagious food distribution. In his model the larvae have no effect on food density, and the model does not use a prey-size-dependent modulation of perceptive field and feeding success. All such models are extremely sensitive to assumptions regarding the perceptive field and swimming speed and to the accuracy of these measurements. For example, Blaxter and Staines (1971) estimated that the searching abilities of herring larvae increase from 0.1 to 2.4 l/hr over 8 weeks, whereas Rosenthal and Hempel (1970) estimated they increase from 1.5 l to about 10 l/hr in 10 weeks. The major difference in these results is in the differences in perceptive distances and rates of swimming (Blaxter and Staines, 1971). It would seem to be of value to use such models to set up hypotheses that could be tested in the laboratory or at sea.

Owing to these problems and to effects of temperature, specific comparisons are difficult, but these estimates do suggest that the volume searched by young larvae is often quite small: pilchard (5–7 mm) search 0.1–0.2 l/hr, plaice (6–10 mm) search 0.1–1.8 l/hr (Blaxter and Staines, 1971), and anchovy (6–10 mm) search 0.1–1.0 l/hr (Hunter, 1972). All studies show that searching abilities increase markedly with growth, since speed, capture success rates, and perceptive distances are functions of length or age.

In the two cases studied, search patterns in larval fishes were nonrandom. Larval anchovy decrease their speed and change their turning probabilities when they enter a dense patch of food. The probability of making a complete reversal in direction increased from 0.04–0.05 at low food densities to 0.23 in dense patches of *Gymnodinium* and to 0.07 in patches of *Brachionus* (Hunter and Thomas, 1974). Wyatt (1972) showed that the time plaice spent swimming increases with a decrease in food density. Similar nonrandom search patterns have been described for adult fishes (Kleerekoper et al., 1970; Beukema, 1968).

Prey

Prey Type

Naupliar through adult stages of copepods are the typical food of most marine fish larvae studied to date. Some notable exceptions to this rule exist: in the North Sea in normal years, the food of plaice larvae consists mostly of the appendicularian *Oikopleura dioica* (Shelbourne, 1962), and larval fishes may be a common item in the diet of the more piscivorous larvae. Larvae are commonly eaten by larval Pacific barracuda (Ahlstrom, personal communication, NMFS, Southwest Fisheries Center, La Jolla) and blue marlin, *Makaira nigricans* (Gorbunova and Lipskaya, 1975); and judging by high incidences of cannibalism under rearing conditions, they may be frequently eaten by many scombroid larvae (Mayo, 1973). Blue marlin larvae begin feeding on fish larvae at 6 mm, and they become the principal food by 12 mm (Gorbunova and Lipskaya, 1975). Under rearing conditions, the scombroid fishes, *Euthynnus alletteratus*, *Scomberomorus cavalla*, *Scomberomorus regalis*, and *Auxis* become cannibalistic at about 5 mm (Mayo, 1973), *Scomber japonicus* at 10 mm, and *Sphyraena argentea* at 4.4 mm (Hunter, unpublished data). Under aquarium conditions, sibling cannibalism appears to end as scombroid fishes become juveniles and begin schooling (Mayo, 1973; Clemens, 1956; Hunter and Kimbrell, 1980a).

Larvae tend to be more euryphagous during the earliest stages and often eat such organisms as tintinnids, phytoplankton, mollusk larvae, and ciliates as well as copepods (Arthur, 1976; Bowers and Williamson, 1951; Lebour, 1921; and Rojas de Mendiola, 1974). Phytoplankton, often identified as green remains, is relatively common in the stomachs of clupeoid larvae at about the time of first feeding but is uncommon soon after. In general, the use of phytoplankton in laboratory rearing studies as a sole source of food for first-feeding larvae has been unsuccessful (May, 1970). Northern anchovy, on the other hand, are able to subsist on a diet of the dinoflagellate *Gymnodinium splendens* for up to 20 days, but at a greatly depressed growth rate (Lasker et al., 1970; Theilacker and McMaster, 1971). Anchovy will feed on a variety of dinoflagellates, *Gymnodinium*, *Gonyaulax*, *Prorocentrum*, and *Peridinium*, but not small flagellates, *Chlamydomonas*, *Dunaliella*, nor diatoms, *Ditylum*, *Chaetoceros*, *Thalassiosira*, and *Leptocylindrus* (Scura and Jerde, 1977). That larvae fed *Gonyaulax* (40 μm diameter) did not survive, whereas those fed *Gymnodinium* (50 μm diameter) did, led Scura and Jerde to conclude that it is the small size of *Gonyaulax* which makes it an inadequate food. Using the same line of reasoning, it seems doubtful that any of the other dinoflagellates they studied would support growth because they are even smaller in diameter.

The tendency for larvae to feed upon a greater variety of organisms in early larval life and subsequent specialization in stages of copepods may simply be due to the existence in the sea of a greater variety of small organisms of the proper size. The ability to subsist on the relatively small organisms such as dinoflagellates may be restricted to larvae of relatively modest energy demand, such as the northern anchovy, i.e., a larva of relatively low initial weight, low activity, existent in cool water.

Prey Size

Size dominates prey selection patterns of larval fishes and is one of the best diagnostic characteristics for evaluating specific ecological roles. The critical dimension for ingestion of copepods and other oblong prey is the maximum width including appendages (Blaxter, 1965; Arthur, 1976). Evidence for this is based on the fact that copepods frequently found in the stomachs of larval fishes are too large to be ingested if length were the critical factor (Blaxter, 1965; Hunter, 1977). Copepods are usually found in the stomachs of clupeoid larvae with antennae folded back along the body (Blaxter, 1965). Blaxter goes on to say that copepods with antennae folded in such a way are probably the only ones that are captured successfully. Inclusion of the appendages increases the maximum width of adult and copepodite stages by about 49% in *Pareuchaeta*, and 25% in *Calanus*, *Pseudocalanus*, *Acartia*, *Microcalanus*, and *Metridia*, but has a negligible effect in *Temora*, *Oithona*, *Oncaea*, and *Microsetella* (Wiborg, 1948a).

The increase in size of prey selected by marine fish larvae as they grow is well documented in the literature and occurs in every species studied. Often, prey length or life stage was used as a measure of size rather than the more informative measurement of maximum prey width. A striking feature of

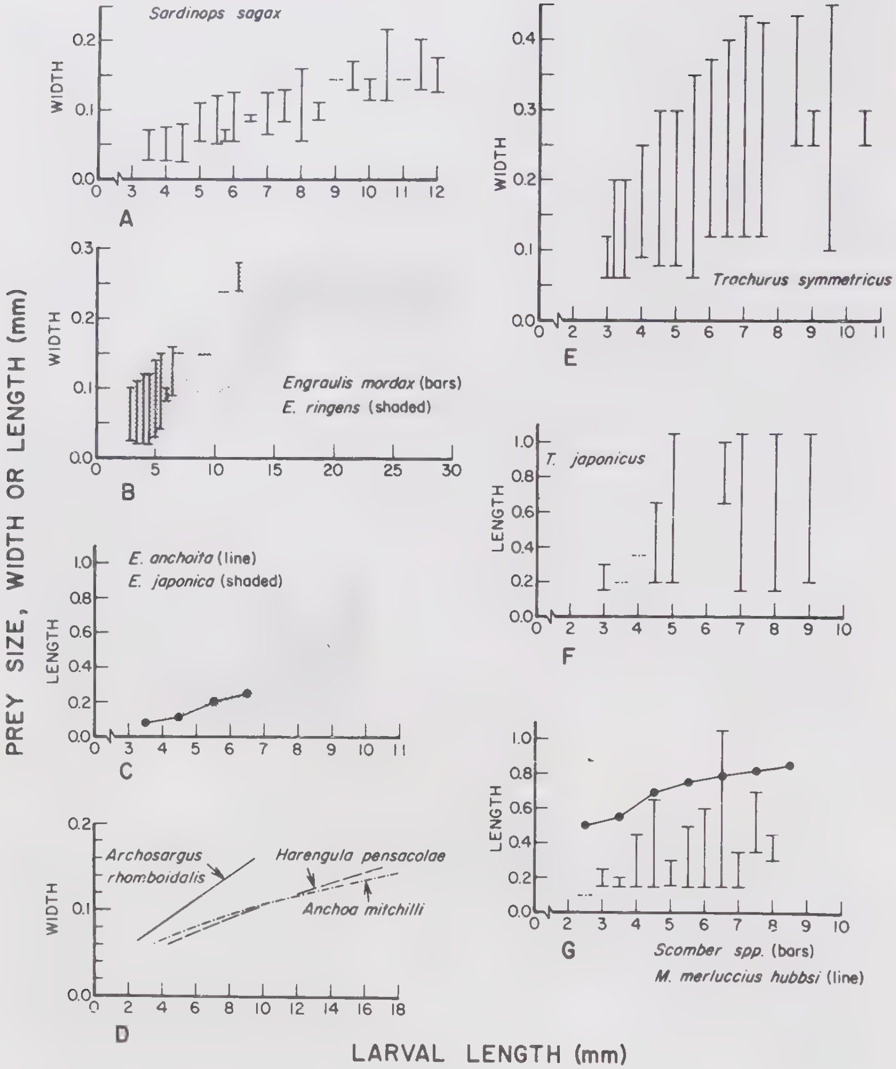

Figure 3. Relation between prey size and larval length for 12 species of marine fishes; label on ordinate indicates whether prey width or prey length were measured; vertical bars and shaded areas represent range of prey sizes; and straight lines connecting dots indicate average prey sizes. Plots were redrawn from Arthur (1976) for *Sardinops sagax*, *Engraulis mordax*, and *Trachurus symmetricus*; from Rojas de Mendiola (1974) for *Engraulis ringens*; from Detwyler and Houde (1970) for *Harengula pensacolae* and *Anchoa mitchilli*; from Stepien (1976) for *Archosargus rhomboidalis*; from Ciechomski and Weiss (1974) for *Engraulis anchoita* and *Merluccius merluccius*; and from Yokota et al. (1961) for *Engraulis japonica*, *Trachurus japonicus*, and *Scomber* spp. Data were for sea-caught larvae except panel D, which were laboratory reared.

these data is the consistency of trends among related species and groups (Fig. 3). The small clupeoid larvae, *Sardinops*, *Engraulis*, *Harengula*, consistently feed on small prey of the order of 50–200 μm width; both species of *Trachurus* show a tendency for a marked increase in the range of food sizes eaten with length, and *Scomber* show a somewhat similar trend. In the three engraulid species, there appears to be a consistent tendency for a marked increase in the range of prey eaten between 8 and 12 mm. Hake larvae, *Merluccius*, begin feeding on much larger foods than the rest, with only a slow increase in average prey size. Ciechomski and Weiss (1974) point out that hake begin feeding on advanced copepodite and adult stages of copepods.

The consistency of these trends from different localities and species strongly suggests that these patterns are the result of positive size selection inherent in species or specific ecological groups of larvae. Stepien (1976) demonstrated that sea bream larvae select foods by size, with a slight positive electivity for prey of 100–200 μm width in larvae 4–5 mm and a stronger positive electivity for prey 200–300 μm in larvae 7–9 mm. The difference between sea bream and the two clupeoid larvae in the figure may be more marked under natural conditions, because the food size preference of sea bream increases faster than the increase in size of the food in the rearing tanks.

Except for hake, specific differences are less marked at the onset of feeding, with all larvae feeding on prey of 50–100 μm width, although jack mackerel take much larger foods as well. Houde (1973) remarks that organisms 50–100 μm are eaten by a great variety of larvae at this time, including those with relatively large mouths such as the tunas and flatfishes. Arthur (1977) estimated the naupliar biomass in the California Current system and expressed it in terms of naupliar width. The naupliar biomass was at a maximum between 50 and 80 μm of naupliar width and declined sharply on either side even though there were many more nauplii of smaller sizes. He points out that the food size ranges of first-feeding Pacific sardine, northern anchovy, and jack mackerel all overlap the naupliar biomass maximum, and it appears that the feeding range of many other larvae do so as well.

Larvae in the above comparisons are relatively the same size at onset of feeding and hatch from relatively small eggs. Larvae from large eggs, for example exocetid larvae and saury (*Cololabis saira*), are 6–7 mm at first feeding and feed on a range of prey equivalent to that of older jack mackerel or *Scomber* of about the same size (Yokota et al., 1961). None of the species in Figure 3, other than hake, could eat newly hatched *Artemia* nauplii at the onset of feeding, but rearing studies reviewed by May (1970) indicate that plaice larvae, two species of *Fundulus*, a species of *Sebastes*, two cottid species, four species of atherinids, *Aulorhynchus flavidus*, and *Fugu pardalis* feed successfully on *Artemia* nauplii at the onset of feeding. Many of these species have large eggs, again emphasizing the importance of the maternal contribution in the feeding tactics of some larvae.

An additional feature of importance in these records is the slow increase

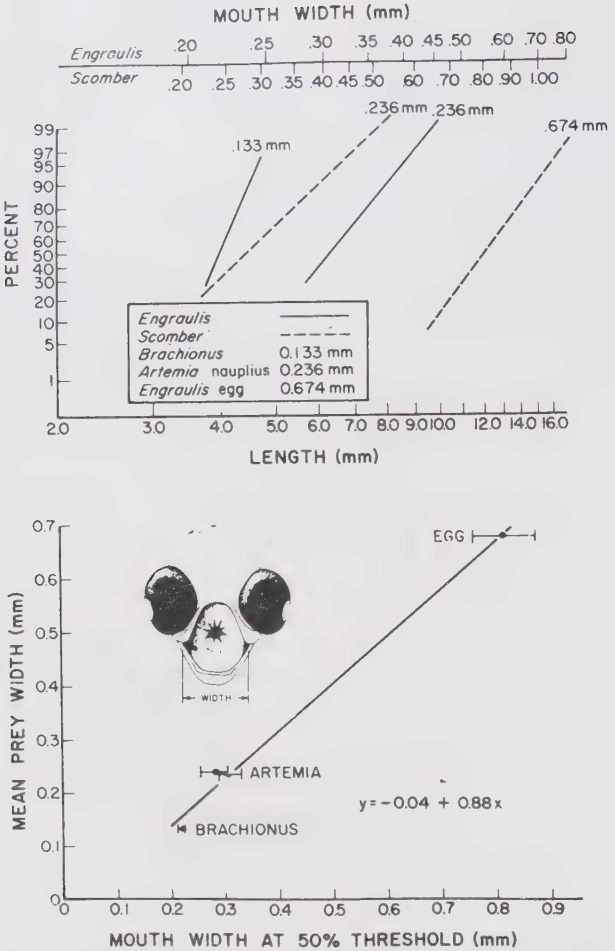

Figure 4. Relation between width of mouth and ability of *Scomber japonicus* and *Engraulis mordax* to capture prey of various widths. Upper panel, percent of larvae that captured one or more prey, shown as a function of mouth width (upper scales) and larval length (lower scale); lines are for the regression of probit on log larval length. Lower panel, average width of prey, shown as a function of the mouth width at which 50% of the larvae ingested one or more prey; estimates taken from probit lines given in upper panel; and bars are the 95% confidence intervals for the estimate. Density of prey in the experiments were: *Brachionus* 9/ml; *Artemia* 10/ml; and *Engraulis* eggs 10/l.

in the minimum size of prey eaten in all species. The effect of this is to greatly expand the prey range in larvae that select larger prey, and this has important energetic consequences. In summary, marine larvae select foods of increasingly larger size as they grow, but the average and range of sizes selected differ greatly among species and may be diagnostic of specific ecological roles.

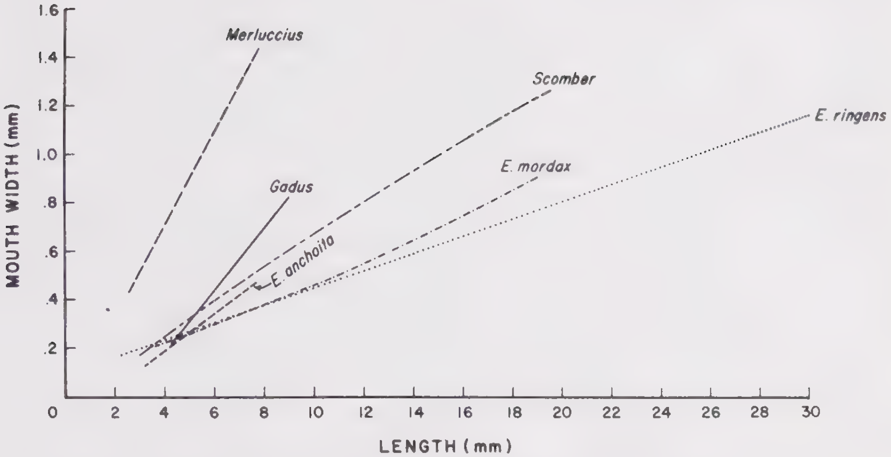

Figure 5. Relation between mouth width and larval length of hake, *Merluccius merluccius*, from Ciechomski and Weiss (1974); cod, *Gadus morhua*, from Wiborg (1948b); Pacific mackerel (*Scomber japonicus*) from Hunter and Kimbrell (1980a) and three species of anchovy, *Engraulis anchoita* from Ciechomski and Weiss (1974), *Engraulis mordax* from Hunter (1977) and *Engraulis ringens* from Rojas de Mendiola (1974).

Effect of Mouth Size

The size of the mouth and the rate it changes with length must be partially responsible for specific differences in food size selection. Shirota (1970) measured the gape of the mouth of 33 species of marine and freshwater larval fishes and correlated them with the size of natural foods and growth rates, and concluded that larvae with smaller mouths grow more slowly than those with larger ones. Blaxter (1965) showed that differences in gape of the mouth exist between different races of herring and concluded that these differences could be of great significance in early survival.

Mouth size would be expected to set the upper size limit for prey. To define this relationship, Hunter (1977) and Hunter and Kimbrell (1980a) determined for anchovy and Pacific mackerel the mouth size threshold for various prey. In these experiments, larvae were exposed to high densities of a single prey—*Brachionus*, *Artemia* nauplii, or anchovy eggs—for 2–4 hours, and the proportion of larvae that captured one or more prey was tabulated by mouth size classes. None of the larvae tested had any previous experience with the particular prey. The width of the mouth was closely correlated with the ability to capture these prey (Fig. 4). The first incidence of feeding occurred when the ratio of prey width to mouth width was close to unity with *Artemia* or anchovy eggs as the prey. In the case of *Brachionus*, it was lower (0.63), which may have been caused by the fact that first-feeding anchovy larvae were used in this experiment to avoid the effect of rapid improvement of success that occurs over the first few days.

These experiments indicated that, on the average, 50% of larval anchovy or mackerel were capable of feeding on these prey when the prey width to mouth width ratio was 0.76. The width of the mouth provided a good indica-

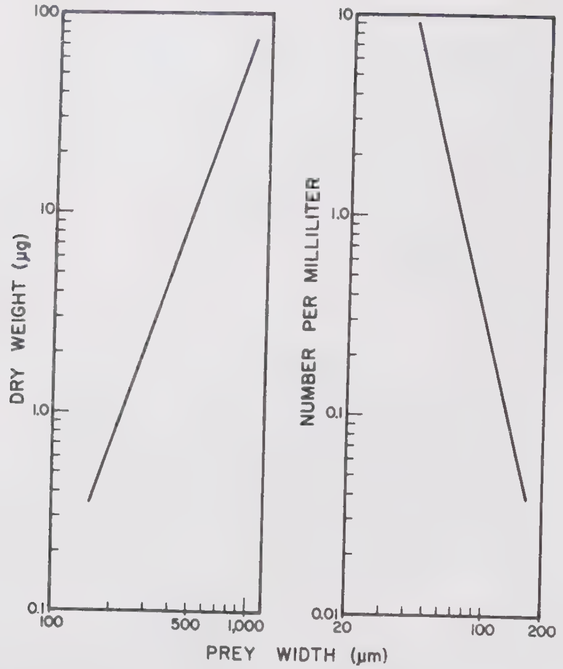

Figure 6. Left panel, relation between copepod width and dry weight (excluding naupliar stages) calculated from data given by Gruzov and Alekseyeva (1970). Right panel, relation between number of prey per ml in the sea and prey width, recalculated from Vlymen (1977).

tion of the size of prey a larva is capable of ingesting. Mouth gape was also measured, but width was preferred because it can be measured with greater accuracy. A different relation could be expected for piscivorous feeding or when ingestion involved manipulation of the prey because larvae are capable of greatly expanding their mouths under these circumstances. The gape of the mouth would be expected to be related to handling time in this case (Kislalioglu and Gibson, 1976b).

These thresholds are of interest because they indicate how feeding success is affected by prey size. They also show that prey are eaten "end first" because at the lowest success levels the prey can be ingested in no other way. Many of the trends in size selection of prey discussed in the previous section are also suggested by the relationship between mouth width and length. The mouth sizes of the three engraulid species are similar to each other and differ markedly from those of the other species (Fig. 5). The mouth widths of all species but hake are somewhat similar in the beginning, but differences increase greatly with growth. Hake stands out as being distinctly different from the rest from the onset of feeding.

The sharp increase in food size that occurs in the engraulids between 8 and 12 mm occurs at a time anchovy become highly proficient in capturing *Artemia* nauplii, and the increase in prey size is to one of that diameter. No

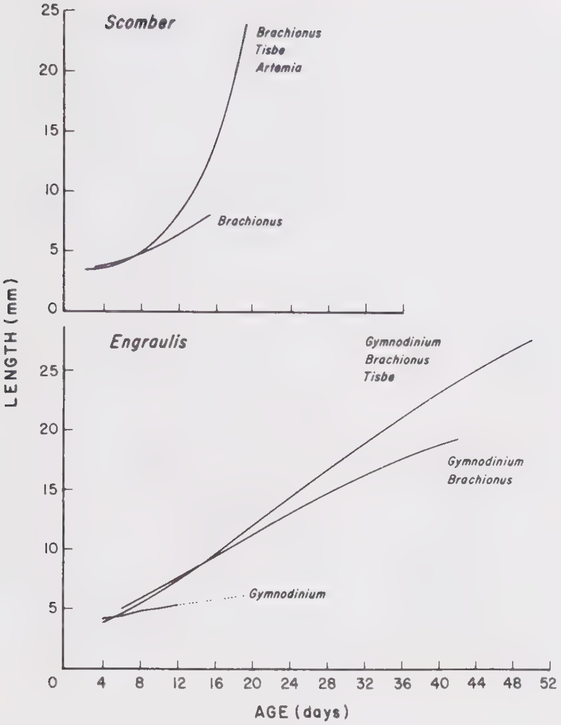

Figure 7. Laboratory growth rates using various foods of *Scomber japonicus* at 22°C from Hunter and Kimbrell (1980a), and of *Engraulis mordax* at 16°C from Hunter (1977). Caloric values of prey were: *Gymnodinium* 0.00005 cal; *Brachionus* 0.008 cal; and Artemia 0.0096 cal.

evidence exists from mouth size information to explain the leveling of food size that occurs thereafter despite the fact that the mouth continues to grow. It seems reasonable to assume larger prey would be eaten if the opportunity existed. Thus, other limits must be imposed; one such limit may be the slow swimming speed of engraulid larvae.

Nutritive Value of Prey of Different Sizes

The nutritive value of larger prey can be illustrated by considering the relation between width of copepods and their weight. Gruzov and Alekseyeva (1970) give a wet weight to length conversion for a group of copepods including species in Calanidae, Paracalanidae, Pseudocalanidae, and other families having a cephalothorax length-to-width ratio ranging from 2.0 to 2.8. I transformed their data to show dry weight as a function of cephalothorax width by using the midpoint of their width ratio (2.4) and assuming a water content of 87% (Lovegrove, 1966). This calculation indicated that an increase of 2.5 in copepod width produces an order of magnitude increase in dry weight. Thus, a larva feeding on copepodites 200 μm wide would have to capture ten times the number of prey to obtain the same ration as one feeding on copepods 500 μm wide (Fig. 6). The effect of a slight increase in width of prey eaten is more marked if the change from feeding on nauplii to copepodites is considered. The change in body width of *Calanus* from nauplius VI to copepodite I is slight even when appendages are included in the measurement (Wiborg, 1948a), but the dry weight doubles. In *Calanus helgolandicus*, the dry weight of N.VI is 2.0 μg and that of C.I is 4.3 μg (Paffenhöfer, 1971). The well-known seasonal and regional variation in copepod weight (Marshall and Orr, 1955; Gruzov and Alekseyeva, 1970) should be considered in any study of food size relations in larval fishes.

The necessity for increasing prey size with growth is illustrated by comparing growth rates of larval anchovy (Hunter, 1977) and Pacific mackerel fed different foods (Fig. 7). When anchovy are fed *Gymnodinium* alone, growth becomes asymptotic at about 6 mm, whereas when *Gymnodinium* and the rotifer *Brachionus plicatilis* are used, growth becomes asymptotic at about 20 mm and few larvae survive (survival drops from 46% at age 26 to 6% at age 42 days). Similarly, Pacific mackerel growth slows on a diet of only *Brachionus,* and few survive beyond 8 mm at age 15 days. Howell (1973) was able to grow plaice larvae through metamorphosis on *Brachionus* alone, but at a much slower growth rate than when *Artemia* was used, indicating that some species are able to grow through metamorphosis on rather small prey, but at a depressed growth rate.

Vlymen (unpublished data, NMFS, Southwest Fisheries Center, La Jolla) estimated for larval anchovy the minimum caloric value of prey required to meet energetic needs for parameters in his 1977 paper. The model uses a 12-hour feeding day, a temperature of 17°C, and the maximum feeding rate observed in the laboratory (about 10 attacks per minute). Gut capacity was not included, and consequently the limit was set by the maximum feeding rate. To calculate the minimum caloric value of prey necessary to meet energy needs, Vlymen used the model

$$E_1 + E_2 + E_3 + E_4 = 0.48R$$

where:

$E_1 = (5.10 \times 10^{-2})\, L^{3.3237}$ (the basic metabolic rate in calories, where L = length in cm);

$E_2 = 0.19\, L^{4.48}$ (the total energy cost of swimming);

$E_3 = 0.05\, L^{4.48}$ (the total energy cost of feeding attacks at maximum rate during a 12-hour day);

$E_4 = 0.29R$ (the energy cost of mechanically processing food, intestinal propulsion, etc.); and

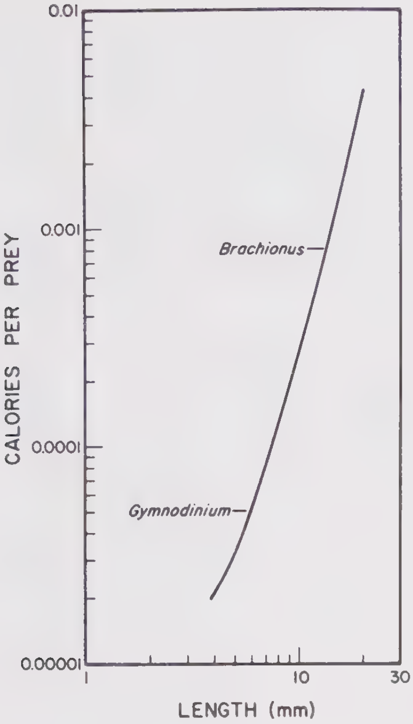

Figure 8. Relation between minimum caloric value of prey required to meet energy needs of larval northern anchovy at 17°C and larval length. From model developed by Vlymen (1977) and Vlymen (unpublished). The caloric value of *Gymnodinium* and *Brachionus* are indicated.

0.48R = the proportion of the ration R available for energetic needs.

The ration at the maximum attack rate was

$$R = (7.12 \times 10^3)\,C \times S$$

where 7.12×10^3 is the total number of attacks at the maximum rate in a day of feeding, C is calories per prey, and S is success of capture. By substitution he obtained

$$(3.78 \times 10^{-5})\,L^{3.3237} + (1.77 \times 10^{-4})\,L^{4.48} = C \times S.$$

The success of capture (S) is a function of age, not length, and is described by the function $S = 93.2 \log_{10} T - 33.3$, where T is larval age in days. To obtain the minimum caloric value of prey for larvae of various lengths, ages at specific lengths were obtained from laboratory growth rates (Hunter, 1976). The origin of the data and the derivation of the parameters used in this model are described by Vlymen (1977).

His results are reasonably close to those described above from rearing work. The model predicts no growth beyond a length of 6 mm on prey having a caloric value of *Gymnodinium* and none beyond 14 mm for *Brachionus*

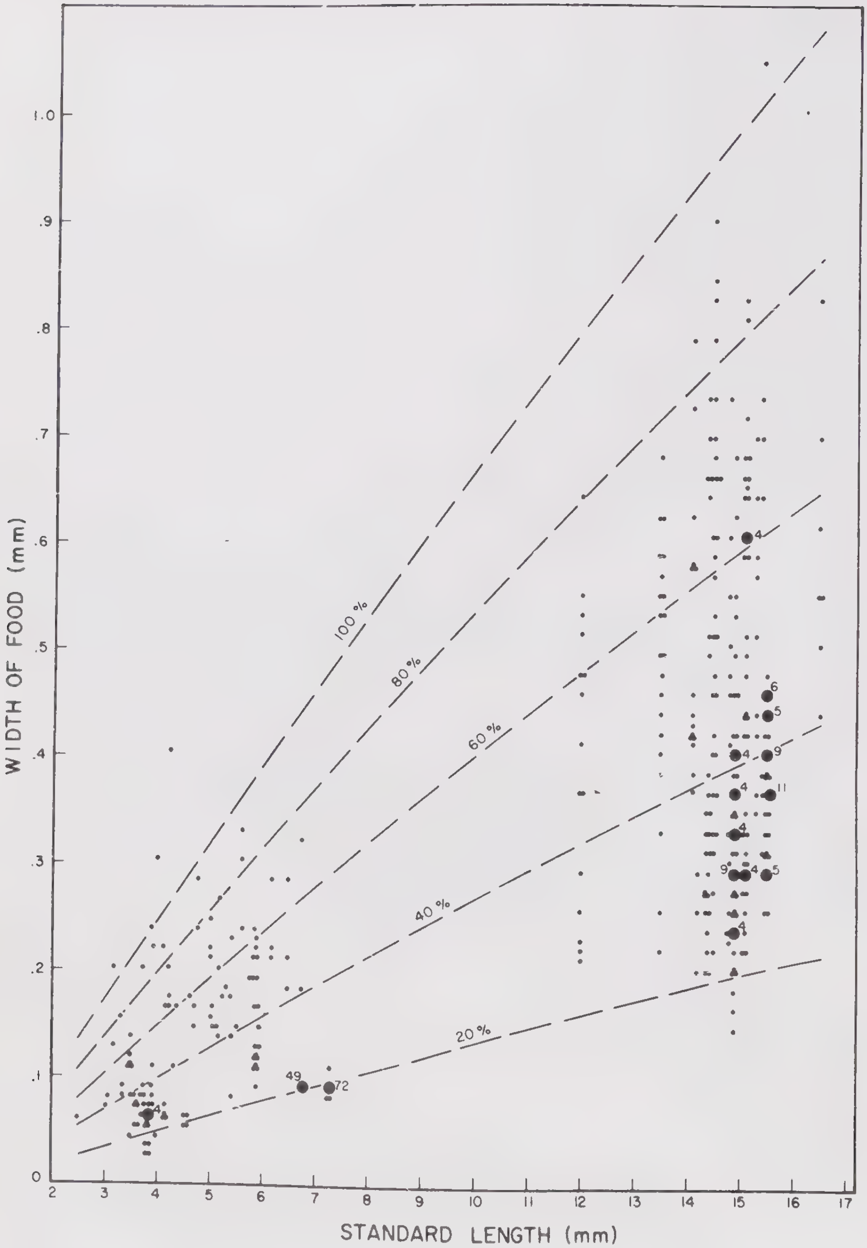

Figure 9. Width of foods eaten in the sea by Pacific mackerel larvae of various standard lengths. Each small point is the width of a single prey; larger points represent multiple points for prey of the same size and number observations. Dashed lines indicate the prey width equal to 20%–80% of the mouth width, or equal to the mouth width (100%), for mackerel larvae of 3–16 mm.

Table 2. Average[a] densities of microcopepods in the sea.

	Average density of microcopepods (number per liter)			
	nauplii	copepodites	total	Location
OPEN SEA	13	2	15	Southeast Coast of Kyushu[b]
	22	36	58[c]	California Current[c]
	40	5	45[c]	Southern California near shore[e]
	27	7	34[f]	Eastern Tropical Pacific[g]
	36	1	37	California Current[h]
PARTLY ENCLOSED	76	19	95	Azov Sea[i]
	—	—	223[j]	Gulf of Taganrog[k]

[a] Mean for all stations and years given in publication listed in table.

[b] Yokota et al. (1961)

[c] Includes all copepods passing 202 μm mesh net.

[d] Beers & Stewart (1967)

[e] Beers & Stewart (1970)

[f] Includes all copepods passing 202 μm mesh net and caught on 35 μm mesh.

[g] Beers & Stewart (1971)

[h] Arthur (1977)

[i] Duka (1969)

[j] Defined as food of *Clupeonella delicatula;* microcopepods account for over 90% of items eaten (Mikhman, 1969).

[k] Mikhman (1969)

(Fig. 8). Thus the lower size limit of prey, at least over the first few weeks of feeding, appears to be set by metabolic relations, whereas the upper limit is controlled by mouth size.

In the sea, many more small prey are eaten than large ones, even in large prey specialists such as Pacific mackerel larvae. Stomach contents of Pacific mackerel from the sea illustrate this point. The mean diameter of prey eaten by these larvae was about 40% of their mouth width (solid line, Fig. 9), although they were able occasionally to eat prey as wide as their mouth (Hunter and Kimbrell, 1980a). If one assumes the prey in Figure 9 to be spherical, which underestimates the size of the larger prey, the small prey that contributed 50% by number contributed only 10%–15% of the total volume of prey eaten. Thus the relatively large and rare prey probably make the major contribution to growth despite the fact that many more small prey are eaten.

Prey Abundance and Density Requirements

The density of particles in the sea declines rapidly with increasing size or diameter of the particle (Sheldon et al., 1972; Sheldon and Parsons, 1967). Such a relationship was presented by Vlymen (1977) for particle size distribution from Niskin casts measured with a Coulter Counter by Richard Eppley

Table 3. Food density thresholds for six species of marine fish larvae.

Species and common name	Container volume (liters)	Duration (days)	Food type	Stock density (No./L)	Survival at various food densities	
					Density (No./L)	Percent survival
PLAICE[a]						
Pleuronectes platessa	5	14	*Artemia* nauplii	50 (larvae)	1,000	72[b]
					500	72
					200	54
					100	32
NORTHERN ANCHOVY[c]						
Engraulis mordax	10.8	12	Wild zooplankton (nauplii)	10 (eggs)	4,000	51
					900	12
					90	0.5
					9	0
BAY ANCHOVY[d]						
Anchoa mitichilli	76	16	Wild zooplankton (nauplii-copepodites)[f]	0.5-2 (eggs)	4,700[e]	65
					1,800	50
					110	10
					60	5
					30	1
SEA BREAM						
Archosargus rhomboidalis	76			0.5-2 (eggs)	2,600[e]	75
					890	50
					130	10
					90	5
					50	1
LINED SOLE						
Achirus lineatus	38			0.5-2 (eggs)	610[e]	75
					220	50
					30	10
					20	5
					9	1
HADDOCK[g]						
Melanogrammus aeglefinus	37.8	42	Wild zooplankton (nauplii)	9[h] (larvae)	3,000	39
					1,000	22
					500	3
					100	0
					10	0

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[a] Wyatt (1972).

[b] Survival was 100% at 50/L for first 7 days without a decrement in length; see also Riley (1966).

[c] O'Connell and Raymond (1970).

[d] Houde (1978).

[e] Estimated food density for indicated survival levels.

[f] Plankton blooms of *Chlorella* sp. and *Anacystis* sp. maintained in rearing tanks.

[g] Laurence (1974).

[h] Estimated by adjusting for hatching success.

(Scripps Institution of Oceanography, University of California San Diego, La Jolla) (Fig. 6). Sheldon et al. (1972) pointed out that roughly similar amounts of organic material exist in logarithmically equal size intervals in any water mass; hence, in any sample, many more small particles exist than large ones. This implies that to feed on larger prey, a larva must search a much greater volume of water, and it also may explain why the minimum and average prey sizes change slowly in larvae that select larger prey.

The density of particles in the size range relevant to larval marine fishes has been studied by a number of workers. Their results have been reviewed by Blaxter (1965), May (1974), and Arthur (1977) and are presented here in Table 2. These studies indicate that average density in the open sea is 13–40 nauplii/l and typically 1–7 copepodites/l. On the other hand, in enclosed areas such as lagoons, bays, and estuaries, much higher densities are found. Average densities in these areas of naupliar and postnaupliar stages combined can exceed 200/l.

Larval fishes have been maintained in the laboratory at various food densities to determine the density of prey required for survival. Some of these density experiments are summarized in Table 3. Most indicate that a prey density of 1,000–4,000 microcopepods/l is required for high survival rates in the laboratory. These results agree in general with what has become standard rearing practice in recent years; in such techniques, the highest densities are used initially and are subsequently reduced to about 1,000/l (Houde, 1973). Much higher densities are required for very small prey such as phytoplankton. Lasker (1975) found that anchovy larvae required 5,000–20,000 *Gymnodinium splendens* cells/l at 19°C and 20,000 or more at 14°C for significant feeding to occur. Standard rearing practice for northern anchovy requires 100,000 or more *Gymnodinium* cells/l (Hunter, 1976b), whereas 1,000 microcopepods/l appear to be adequate (O'Connell and Raymond, 1970).

Density thresholds determined by Houde (1975, 1977, 1978) are markedly lower than those of the others listed in the table and are substantially below those used for routine rearing of larval fishes. Houde attributes his lower thresholds to use of lower stocking densities, general improvement in culture techniques, and frequent daily monitoring and adjustment of food density. He also maintains a dense phytoplankton bloom in his containers, which may also contribute in some way to higher survival. Of particular interest is the very low threshold determined for sea bream, emphasizing the importance of specific feeding tactics. This species selects larger prey (Stepien, 1976) than the other species studied by Houde and, judging by the density threshold, is much more efficient in finding and catching prey.

In general the density thresholds determined for larvae in the laboratory are much higher than average microcopepod densities in the open sea, described in the preceding section. On the other hand, the high microcopepod densities in enclosed areas are within the range that Houde (1975, 1977) found to support survival and growth. Thus food may not be as critical for species such as those he studied, which exist in enclosed areas. Many problems exist in interpreting laboratory findings and extending them to field conditions. The interactions of stock density, food density, and mortality are problems which may be overcome to some extent by use of low stocking densities and frequent monitoring of food density. Changes in ration with development and prey size distributions in the tank are also critical. The few larvae that survive at very low prey densities may be those that captured, either by good fortune or because of a larger mouth, the few larger prey in the container. Selection of the appropriate criteria also poses problems. Growth as well as survival declines with food availability; this is evident in all the food density studies cited but perhaps best illustrated by Riley (1966), Wyatt (1972), and Houde (1975, 1977). Reduction of growth may be nearly as lethal as starvation because of the increased exposure to predation.

Patchiness

The disparity between most estimates of food densities required by larvae and average densities in the open sea has led to the hypothesis that larvae may be dependent on small-scale patchiness of food. In the sea, large-scale sampling will always tend toward the mean concentration between such patches. Data collected by Yokota et al. (1961) on naupliar abundance provide one of the better examples of patchiness of larval forage because the samples were taken on a scale relevant to larval searching behavior. They counted all the nauplii occurring in one-liter samples taken at the surface from an area off the southeast coast of Kyushu over two years. The average naupliar density for their 4,730 samples was 13/l. The greatest number in a single sample was 524, and only 2% of the samples accounted for over 20% of the nauplii.

Laboratory experiments on searching behavior discussed previously indicate that larva have the ability to remain in patches of food if they find them. The search model of Vlymen (1977) indicated that the average anchovy larva could not exist in the sea if food were distributed randomly. He concluded that first-feeding anchovy larvae require a food contagion of $K = 0.17$, where K is the negative binomial, just to meet minimum energy requirements. To meet minimum requirements, therefore, prey would have to be 1.3 times as "crowded" as they are on the average, if the population had a random distribution (Lloyd, 1967).

Lasker (1975) tested the patchiness hypothesis by exposing anchovy larvae to samples of water taken from the surface and from the chlorophyll maximum layers usually 15–30 m below the surface. Feeding by larvae was minimal in samples taken from the surface, but extensive feeding occurred in water from the chlorophyll maximum layer when these samples contained prey of about 40 μm at densities of 20,000–400,000 prey/l. The prey were primarily the phytoplankter *Gymnodinium splendens;* microcopepods were never at high enough densities to be eaten by the larvae. Houde and Schekter (1978) exposed sea bream to simulated patch conditions in the laboratory by increasing the concentration of microcopepods to 500/l for periods of 2–13 hours per day from a background density of 25–50/l. They found that survival at 10 days after hatching of larvae exposed to only three hours of food at 500/l was similar to that of larvae fed at a constant 500/l. Thus, even very short-term patchiness could enhance survival in this species. Lasker (1975) has considered a much broader time scale; the bloom of *Gymnodinium* had persisted for at least 18 days until a storm obliterated the chlorophyll maximum layer. His measurements after the storm indicated that the density of food was insufficient for feeding.

If patchiness of food is a key to larval survival in the open sea, one could expect survival and growth of larvae to show considerable small-scale patchiness within the species spawning region. Present evidence for northern anchovy larvae supports this view. O'Connell (1981) measured the incidence of starvation of larval anchovy in the sea using histological techniques that had been calibrated by starving larvae in the laboratory (O'Connell, 1976). He found that 8% of larval anchovy in the Los Angeles Bight in March were in poor histological condition, indicating that death from starvation was imminent. For larvae of the size he studied (about 8 mm SL) this could represent about 40% of the daily rate of mortality. Of great importance to this discussion is the high variability that existed in the condition of larvae occurring in different tows. In some tows, 60% of the larvae were starving, yet all larvae in tows taken a few nautical miles away were in excellent condition. Thus as much variability in starvation existed within a few nautical miles as existed over the entire Los Angeles Bight. Similarly, Methot and Kramer (1979) found as great a difference in growth of anchovy larvae (estimated from daily increments of otoliths) in samples taken a few nautical miles apart as among all samples taken in the Bight area. Thus larval foods, larval growth, and starvation all appear to exhibit small-scale patchiness. It may be the summation of such small-scale events over time and space that ultimately determines the success of a year class.

Predation

Little literature exists that is concerned specifically with predation on pelagic egg and larval stages of marine fishes. Many species within the major groups of pelagic invertebrates, including Medusae, Siphomedusae, Ctenophora, Chaetognatha, Cephalapoda, hyperiid amphipods, euphausiids, and carnivorous calanoid copepods, as well as pelagic fishes, have been reported to feed on the eggs and larvae of marine fishes. That predation exists is amply documented by food habit studies of organisms in these groups as well as by some aquarium observations, but most studies give no indication that the predation by a species is a significant part of natural larval mortality. The records of egg and larval predation are drawn primarily from general descriptions of food habits of the predators, and incidence of predation is often summarized without regard to the seasonal changes in larval and egg abundance. On the other hand, these studies indicate that larval fishes and eggs typically constitute a small and highly variable proportion of the foods usually eaten.

Estimates of mortality of egg and yolk-sac stages indicate that predation must be very high. Starvation can be eliminated as a source of mortality in these stages because larvae subsist on their yolk. Losses range from 10% to 95% per day and typically are 30%–40% (Jones and Hall, 1974; Vladimirov, 1975; Riley, 1974). Although predation is possibly the largest source of mortality in larval fishes, it remains at present largely undocumented.

In this lecture I will first discuss characteristics of the behavior of the parents and the larvae that affect vulnerability to predation and then consider the evidence for effects of specific marine predators. I restrict my presentation to predation in the pelagic realm, recognizing that predation on demersal eggs of marine fishes is often a major source of mortality. The larvae of many demersal spawners are pelagic, however, and may encounter the same groups of predators as those of pelagic spawners.

Factors Affecting Vulnerability

Parental Behavior

The spawning behavior of the parents affects the vulnerability of pelagic eggs and larvae to predation. These influences include the time and location of spawning and the density of eggs. Nocturnal spawning occurs in many clupeoids (Blaxter, 1970); in the northern anchovy, for example, spawning begins at sunset, reaches a maximum about midnight, and declines thereafter (Hunter and Goldberg, 1980; Hunter and Macewicz, 1980). Johannes (1978) concludes that the majority of tropical marine fishes with pelagic eggs spawn at twilight or night and suggests that this may reduce the intense predation by diurnal planktivores in tropical reef communities, because eggs are transported by currents into the open sea away from inshore planktivores. Hobsen and Chess (1978) reported that pelagic fish eggs are an important component of the diet of diurnal planktivores at Enewetak but were insignificant in diets of nocturnal planktivores. In the open sea, nocturnal spawning may also reduce vulnerability to predation because it permits some dispersion of egg patches before they become vulnerable to diurnal planktivores. The dense egg patches produced by clupeoid fishes may increase vulnerability because predators could converge on such patches and feed selectively on eggs and larvae.

Vulnerability to predators may also be reduced by the location of spawning. Johannes (1978) points out that many tropical reef fishes spawn in localities (on the outer reef slope, near channel mouths, in open water, and at other sites) where eggs are transported by currents away from the intense predation of the reef. Northern anchovy may spawn in areas in the open sea that have fewer large planktonic predators (Alvariño, 1980), a topic discussed in greater detail further on.

Starvation

It is generally believed that a prudent predator would select prey that are about to die anyway, that is, the youngest ones and those weakened by starvation or other causes. No information exists on the effect of starvation on vulnerability to predation of marine fish larvae, but one might expect it to vary with effect of starvation on sustained high-speed swimming. Laurence (1972) observed that the maximum speed that starved largemouth bass larvae, *Micropterus salmoides*, could sustain for 30 minutes declined with starvation, from about 3 to less than 2 body lengths per second, whereas the sustained speed of fed larvae was about 4–5 lengths per second. Ivlev (1961) in his classic work on the feeding ecology of fishes provides an example for freshwater juveniles and fry. Ivlev found that the effect of starvation on the vulnerability of roach fry to pike was strongly size dependent. Starvation of 10 cm roach fry had little effect on the vulnerability to predation by 12–15 cm pike, whereas predation doubled when 29 cm roach fry were starved. Ivlev goes on to say that the relation between starvation and vulnerability was similar in form to the swimming fatigue curve for roach fry (flow rate fish could sustain for 5 minutes), implying that a decrement of swimming ability caused by starvation was equivalent to a decrement in avoidance. An important conclusion that can be drawn from Ivlev's work is that the decrement in avoidance behavior caused by starvation is probably important only when the difference in size between predator and prey is not great.

Larval Size and Time of Day

Catch data from plankton nets illustrate that avoidance capabilities appear to increase exponentially with larval length. Murphy and Clutter (1972) compared the daytime catch of tropical anchovy, *Stolephorus*, taken in one-meter plankton nets with that taken at about the same time in a plankton purse seine. The ratio, purse seine catch to one-meter net catch, increased markedly with larval length after anchovy attained a length of about 5 mm (Fig. 10). The ratio of night catches in plankton nets to day catches follows a similar exponential trend with length in several other clupeoid fishes. That Murphy and Clutter's data for daytime avoidance are about the same as the day/night ratios for plankton net catches of clupeoids indicates that the apparent exponential form of the relation is not entirely the result of improvement in nocturnal vision. Recent work by Paul Webb (unpublished data, University of Michigan, Ann Arbor, Michigan) indicates that maximum speed of burst-swimming in anchovy larvae increases at a rate proportional to larval length times 20 and the duration of such bursts by length times 4. An explanation for the exponential increase in avoidance capabilities with length in clupeoid larvae is that avoidance is a function of both absolute speed and the duration that larvae are able to sustain that speed, as both factors increase with length; when combined they might yield an exponential relation.

In the more robust, fast-swimming larvae, such as jack mackerel and Pacific mackerel, day/night differences in catch are barely detectable. These larvae are able to escape almost as well by night as by day. The rapid decline of the catch curve of jack mackerel larval length in comparison with clupeoid larvae suggests that these more robust and fast-swimming larvae have a much greater avoidance ability (Lenarz, 1973). Few jack mackerel or Pacific mackerel larger than 7–8 mm are taken in routine oblique plankton tows (P. Smith, unpublished data, NMFS, Southwest Fisheries Center, La Jolla, Ca.).

Clupeoid larvae, as well as other species, do not develop a functional scotopic visual system until late in larval life (Blaxter, 1968a, 1968b; O'Connell, 1981); hence they would be more vulnerable to predators at night than in the day, as the day/night ratio of catch indicates. Murphy and Clutter (1972) also show that anchovy larvae avoid nets at night; however, detection of the net and perhaps predators at night, may be dependent on lateral line sense, because the lateral line is functional at hatching in anchovy (O'Connell, 1981). Vulnerability at night may also increase if larvae enter a less responsive state. Adult fishes have been shown to be less responsive to olfactory alarm stimuli at night than in the day (Thines and Vandenbussche, 1966). Anchovy fill their swimbladder at the water surface at night and remain relatively inactive, supported by the distended swimbladder until dawn (Hunter and Sanchez, 1976). Larval *Blennius pholis* survival was lower when maintained under continuous light than when given a daily light cycle (Qasim, 1959). These studies indicate existence of a diel rhythm in activity, and thus larvae might be less reactive to stimuli at night because of a different reactive state, but definitive evidence does not exist.

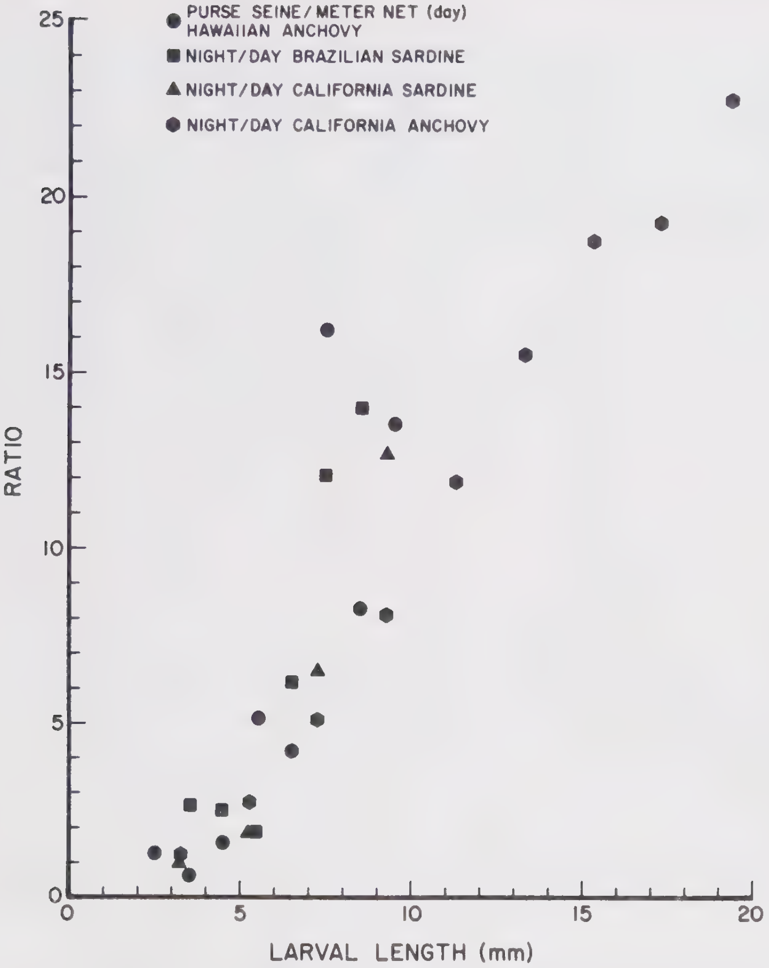

Figure 10. Change in avoidance ability of four species of clupeoid larvae with length. Avoidance ability indicated by the ratio of purse seine to 1-m net catches of the Hawaiian anchovy, *Stolephorus purpureus* (Murphy and Clutter, 1972); and by the ratio of night to day plankton net catches of the Brazilian sardine, *Sardinella brasiliensis* (Matsuura, 1977), California sardine, *Sardinops sagax;* and California anchovy, *Engraulis mordax* (Paul Smith, unpublished data, NMFS, Southwest Fisheries Center, La Jolla.)

State of Maturity

Maturation of sensory and locomotor systems must affect the ability of larvae to avoid predation. Although maturation continues throughout the larval phase, the greatest changes occur during the yolk-sac period. In northern anchovy larvae at hatching, innervation of the Mauthner cells is incomplete, the eye is nonfunctional (O'Connell, 1981), and activity consists of relatively long periods of rest, interrupted by brief periods of vigorous swimming (Hunter, 1972). By the end of the yolk-sac stage, innervation of the

Mauthner cells is complete, and the larva becomes capable of the rapid startle response of most teleosts (Eaton et al., 1977); the eye becomes functional for daytime vision, and the larva is almost continually active in the day. One would expect vulnerability to predators to decrease as these developmental events occur; this seems to be supported by laboratory evidence. The ability of copepods (Lillelund and Lasker, 1971) and euphausiid shrimp (Theilacker and Lasker, 1974) to capture yolk-sac larvae in the dark declined markedly over the yolk-sac period. For example, the feeding success of *Euphausia pacifica* declined from 60% for 1–2-day-old yolk-sac larvae to 17% for 3-day-old larvae and 11% for 4-day-old larvae. Theilacker and Lasker (1974) suggest that this decline is related to the increase in larval activity, because small predators such as copepods and euphausiids may be unable to capture moving prey and it is the long periods of rest that make larvae vulnerable to these predators.

Types of Predators

Planktonic Invertebrates

Consumption of marine fish larvae by marine copepods, euphausiid shrimps, hyperiid amphipods, and chaetognaths has been studied in small containers in the laboratory. Lillelund and Lasker (1971) showed that 11 species of calanoid copepods were capable of capturing or fatally injuring yolk-sac anchovy larvae. The number of yolk-sac anchovy killed by a *Labidocera jollae* female declined with larval age from 16 newly hatched larvae per day to about 7 for 168-hour-old larvae, and from about 5 larvae to 1 for *L. trispinosa* females. The median number of yolk-sac anchovy larvae eaten by the euphausiid shrimp, *Euphausia pacifica*, was 2 per day when the density of larvae exceeded 1 per 3,500 ml (Theilacker and Lasker, 1974); and at a density of 50 yolk-sac herring larvae/50 ml, the hyperiid amphipod, *Hyperoche medusarum*, attacked larvae at a rate of 0.45/hour (Westernhagen and Rosenthal, 1976). Two species of chaetognaths, *Sagitta elegans* and *S. setosa*, consumed on the average 1.5 fish larvae after a 48-hour starvation period, but larvae were not taken in significant numbers if the chaetognaths were not starved at least 24 hours (Kuhlman, 1977).

In *Sagitta* (Kuhlman, 1977) and *Labidocera* (Lillelund and Lasker, 1971), the number of larvae eaten or attacked was found to be independent of larval density as long as the density exceeded a certain minimum; on the other hand, in *Hyperoche* (Westernhagen and Rosenthal, 1976) and *Euphausia* (Theilacker and Lasker, 1974), the number of larvae attacked increased initially with larval density, then became asymptotic with density, the type two predator response of Holling (1966).

Probably only yolk-sac larvae are vulnerable to attacks of *Labidocera*, *Euphausia*, and *Hyperoche*, because older larvae easily avoided attack even in the small containers used in these studies. The two species of *Sagitta* are restricted to an even smaller size range because yolk-sac larvae were not attractive, presumably because of their lack of movement (Feigenbaum and Reeve, 1977), and larvae older than 4 days easily escaped. These small predacious invertebrates feed, of course, on foods other than fish larvae; the number of anchovy eaten by *Labidocera* declined in proportion to the density of the alternate food (*Artemia* nauplii), and *Sagitta* showed a strong preference for copepods when both copepods and larvae were offered (Kuhlman, 1977). *Hyperoche*, however, showed a strong preference for herring yolk-sac larvae over flatfish larvae.

It seems unlikely that *Sagitta setosa* and *S. elegans* have a significant impact on larval fish populations. In addition, Cushing and Harris (1973) conclude that chaetognaths are present in sufficient numbers to account for a larval mortality of only 1% per day. On the other hand, hyperiid amphipods, *Labidocera*, and *Euphausia* may be significant predators on yolk-sac stages of fish larvae. The first of the year populations of *Hyperoche* co-occur for 40 days with yolk-sac herring larvae, and fish larvae remains are the most abundant item in their gut (Westernhagen, 1976). In addition, Sheader and Evans (1975) report that fish larvae, especially *Clupea* and *Ammodytes*, make up 23.4% of the food of the hyperiid amphipod, *Parathemisto gaudichaudi*, during April and June. Both *Euphausia* and *Labidocera* co-occur with anchovy larvae along the California coast, but no food habit studies exist. Theilacker and Lasker (1974) estimated from the abundance of *Euphausia* and their median feeding rate in the laboratory that *Euphausia* could consume 2,800 anchovy larvae per day per square meter of sea surface, which is more than 40 times the average number of yolk-sac anchovy existent per square meter.

Certainly the potential predation by these small planktonic predators could have a significant effect on survival of early yolk-sac stages, but larger and more agile predators are required for older larval stages. Larger planktonic predators could include some of the larger Chaetognatha, Siphonophorae, Chrondrophorae, Medusae, and Ctenophora. No detailed studies on the impact of these larger invertebrate predators exist, although incidental observations of feeding behavior and food habit studies are available (Lebour, 1922, 1923, 1925; Frazer, 1969; and others).

Alvariño (1980) tabulated the abundance and co-occurrence with northern anchovy larvae of five major groups of large invertebrate predators—Chaetognatha (22 species), Siphnophora (48 species), Medusae (20 species), Ctenophora (4 species), and Chondrophorae (1 species)—taken in over 2,000 routine ichthyoplankton tows off the California coast in 1954, 1956, and 1958. In general, the abundance of all species combined showed an inverse relation to the abundance of anchovy larvae; that is, these potential predators were the most abundant in tows when anchovy larvae were not taken or were less abundant than average. To pursue this analysis further, she selected among the species those she felt to have the highest potential as larval predators because of their size, abundance, and feeding habits. These planktonic

Table 4. Most abundant large planktonic invertebrate predators taken in standard oblique plankton hauls along the California coast in 1954, 1956, and 1958 and their occurrence with larval anchovy (from Alvariño, 1980).

	1954				1956				1958			
Abundance of anchovy larvae:	High[a]		Zero		High[a]		Zero		High[a]		Zero	
Species abundance:	Frequency (%)[b]	Mean number[c]	Frequency (%)[b]	Mean number[c]	Frequency (%)[b]	Mean number[c]	Frequency (%)[b]	Mean number[c]	Frequency (%)[b]	Mean number[c]	Frequency (%)[b]	Mean number[c]
Chaetognatha												
Sagitta enflata	56	491.3	73	1093.7	43	191.8	47	121.6	74	271.6	82	308.4
S. hexaptera	22	5.5	55	16.1	27	1.8	53	62.0	26	15.5	52	42.2
S. scrippsae	33	48.1	52	19.2	20	3.2	33	17.4	16	6.5	27	9.9
Siphonophorae												
Stephanomia bijuga	7	0.2	27	0.8	13	1.2	22	2.0	11	0.2	27	1.8
Chelophyes appendiculata	33	10.0	76	89.3	17	5.0	47	7.6	32	2.6	67	46.2
Diphyes dispar	22	14.7	48	44.1	0	0	0	0	0	0	3	0.4
Medusae												
Liriope tetraphylla	22	20.9	64	253.6	37	96.5	42	41.8	21	6.8	58	89.4
Rhopalonema velatum	7	0.6	46	30.3	7	0.3	28	4.1	5	0.3	33	18.2
Aglaura hemistoma	0	0	12	40.2	0	0	3	1.1	5	0.2	18	51.7

[a] Greater than the average number of anchovy per positive haul (241 anchovy larvae per 10 square meters of sea surface).
[b] Percent of stations in which species occurred.
[c] Average number of individuals taken in positive stations.

predators occurred much less frequently and at lower abundances where anchovy were abundant and usually occurred most commonly where no anchovy larvae were taken (Table 4). The dominant constituents in collections where anchovy were abundant were copepods and euphausiids, whereas collections without anchovy were dominated by jelly-like plankters, salps, doliolids, and pyrosomes. Thus, anchovy spawn most intensely in areas where large planktonic predators capable of feeding on post yolk-sac larvae were rare and where foods for the adults and larvae were abundant (copepods and euphausiids).

In sum, planktonic invertebrate predators do not appear to be an important source of mortality for anchovy larvae other than during the yolk-sac stage. These predators may have an important effect on other fish larvae, however, but no adequate documentation exists. Squid, *Loligo opalescens*, might be an important predator of anchovy larvae; they co-occur with anchovy (Cailliet et al., 1979) and feed upon them, but *Euphausia* is their principal food (Karpov and Cailliet, 1978).

Fishes

Perhaps the most important group of predators of marine fish eggs and larvae are schooling pelagic juvenile and adult fishes. Analysis of stomach contents of such fishes usually indicates they do indeed eat larval fishes and eggs. It would be a formidable task to review this large literature, but I will cite a few examples for clupeoid fishes, the most important group of larval and egg predators because of their abundance, schooling behavior, and planktonic feeding habits.

Larval sand eel, *Ammodytes* (ca. 33 mm), comprise about 10% of the total food items eaten by North Sea herring in the Shields area from 1930 to 1934 (Savage, 1937) and about 42% of the food organisms eaten by herring from the southern North Sea and Tyne area (Hardy, 1924). Both authors cited found a variety of other fish eggs and larvae in herring stomachs as well, but at lower abundances. More recently, Pommeranz (in press) observed that at one station 54% of the wet weight of the stomach contents of herring and 45% of that of spratt (*Sprattus sprattus* L.) were composed of fish eggs and larvae. Average values for eggs in herring stomachs ranged from 0.03% to 51.1% (on the average, about 4 eggs per stomach) and the proportion of fish larvae from 0% to 3%. Harding et al. (1978) found that stomachs of herring taken in egg patches in the North Sea contained about 3% fish eggs and 62% fish larvae.

Feeding of the scombrid (*Rastrelliger kanagurta*) on the eggs of the labrid (*Thallusoma*) has been actively observed by Colin (1976). *Thallosoma* engaged in mass spawning which involved an upward rush and visible release of eggs and sperm; about five *Rastrelliger* converged on the site and began filter feeding on the eggs while swimming in tight circles.

My observations of the feeding behavior of northern anchovy are nearly identical to those of Colin (1976); when anchovy eggs were added to a tank, the school swam over the area and began filtering intensively while swimming in an elliptical orbit through the egg patch. Many reports exist for anchovy feeding on eggs and larvae of marine fishes including their own. In southern California, the most abundant pelagic planktivorous fish is the anchovy, hence they may be one of the major predators of fish eggs and larvae in the open sea. In a recent study (Hunter and Kimbrell, 1980b), stomach contents of anchovy taken during a peak spawning month contained on the average 5.1 anchovy eggs per fish. They used these data to calculate a daily ration of eggs of 86 eggs per fish and estimated that this represented about 17% of the eggs spawned per night, or about 32% of the daily mortality of eggs. They point out that the number of anchovy eggs in stomachs increased exponentially with the density of eggs in the sea, indicating that patchiness of eggs and selectivity of filtering by the schools probably play a major role in egg consumption. Very few larvae of any species occurred in the stomachs, but Hunter and Kimbrell's laboratory observations indicate that the smallest and most abundant anchovy larvae (3–5 mm SL) are digested beyond recognition in less than half an hour, whereas eggs are more resistant to digestion. Although no evidence exists, I believe that the younger larval stages are as vulnerable as eggs. Larvae probably remain highly vulnerable to schooling planktivorous fishes until avoidance abilities develop sufficiently. Yolk-sac larvae are readily eaten in the laboratory by anchovy, and their low incidence in field-caught specimens is probably the result of the rapid digestion rate and the decline in patchiness and abundance.

Conclusions

An understanding of the causes of larval mortality demands a thorough understanding of early life history traits. Traits discussed in these lectures include parental factors of time and place of spawning, pattern of spawn distribution, egg size and yolk reserves and such larval characters as feeding behavior, prey selection patterns, swimming and searching behavior, metabolism, growth rate, and time to the onset of schooling. These traits are interrelated and consequently form distinct life history strategies.

Food size preferences may be one of the better traits for identifying life history strategies. For example, to feed on a large prey requires a large mouth and a greater and more efficient effort because of the exponential decline in food density with food size. Persistence in attack and maneuverability would appear to be essential for a large prey strategy. Greater searching effort may require a faster swimming speed, and this in turn implies less vulnerability to predation and higher metabolic rate and energy requirements. The latter promotes faster growth (Kerr, 1971a, 1971b), and faster growth reduces the duration of the larval stage, the period of greatest vulnerability to predation, and the time to the onset of schooling. Mackerel and tunas appear to have adopted this large prey-fast growth strategy, whereas anchovy follow a small prey strategy. The sparid *Archosargus rhomboidalis*, which seems to fit in many respects the large prey feeding strategy, is affected much more by laboratory stocking density and is better able to take advantage of short-term patchiness of food than is the engraulid fish *Anchoa mitchilli* (Houde and Schekter, 1978). These tendencies are in keeping with the difference in searching power and efficiency of feeding implicit in large and small prey feeding strategies.

At high spawn densities, suppression of intraspecific effects on growth would be adaptive as well as suppression of sibling cannibalism. Species with slow cruising speeds, such as anchovy, might require higher initial larval densities to assure the socialization necessary for the onset of schooling or to form schools of viable size. Mackerel and tunas, on the other hand, are prone to sibling cannibalism and may not be affected by low spawning densities because the time to school formation is less, because growth is rapid and cruising speeds are higher, thus permitting more rapid formation of schools. Many other possible strategies exist other than those discussed for anchovy and scombroids. Species that hatch from large eggs in a relatively large and mature stage—flying fish, herring larvae, and saury, for example—have distinctly different life strategies.

My emphasis in these lectures on feeding ecology was on specific differences and how they form distinct life history strategies in the larval phase. The apparent similarities in feeding habits among pelagic larvae are striking nonetheless. Nearly all pelagic larvae are diurnal particulate planktivores, specializing in the young stages of copepods, whereas the feeding habits of the adults are much more diverse. Pelagic fish larvae are the most similar in the early stages of development, and distinctions become marked as development proceeds and larvae approach metamorphosis.

The literature I have reviewed on feeding ecology and on predation in larval fishes indicates that the smallest life stages are without doubt the most vulnerable to starvation and predation. Low feeding success, low resistance to starvation, and slow absolute swimming speeds all indicate that larvae are more vulnerable to starvation at the time of first feeding than at any other time. Similarly, the ability to avoid predation is dependent on burst speeds, the ability to sustain that speed, and the developmental state of sensory and locomotor systems. All of these improve rapidly with larval size or age. In addition, the number of potential predators may decrease with an increase in larval size; the highest number may occur during the yolk-sac period when larvae may be eaten by small planktonic invertebrates as well as by larger invertebrates and fishes.

Although the high early mortality of marine larvae is documented (May, 1974; Jones and Hall, 1974; Vladimirov, 1975), no conclusive evidence exists that variation in the rates of early mortality determines the strength of incoming year classes. This idea, Hjort's critical period concept (Hjort, 1914; May, 1974; Vladimirov, 1975), has long been postulated as a mechanism for variation in year class strength. It now appears, at least for the northern anchovy, that except for a few extreme cases it is not possible to detect changes in recruitment potential from the abundances of embryonic or postembryonic larvae up to 15 mm in length (Zweifel and Smith, in press). Thus identification of mechanisms regulating recruitment will probably require study of the entire larval and juvenile stages.

A recurrent theme in these lectures has been the role of patchiness in the early life history of fishes. Patchiness affects food availability which in turn may produce patchiness in larval survival and growth. Although direct links between food patches and survival have not been documented, the circumstantial evidence is strong. Larval food exists in patches (Lasker, 1975), and small-scale patchiness in growth and starvation exists (Methot and Kramer, 1979; O'Connell, 1981). Patchiness may also affect vulnerability to planktivorous predators, the onset of schooling behavior, and sibling cannibalism.

If patchiness controls larval survival, variation in recruitment ultimately may be the result of the summation of events occurring in a multitude of egg and larval patches. Although this increases the complexity of the problem, techniques now exist to study it. It is now possible to make reliable instantaneous estimates of the incidence of starvation (O'Connell, 1976, 1981; Theilacker, 1978) and of larval growth (Buckley, 1980; Methot, in press). Such estimates need to be related to the condition of the plankton community from which they were taken. Measures of community condition, such as standing crop of microcopepods, indices of naupliar production rate, primary production, oxygen, and nutrients, and other biotic and abiotic characteristics need to be related to instantaneous growth rates and starvation from the same patch. Such a dynamic description of the local community or patch condition could then be used to calibrate oceanic events in terms of larval growth and survival. In addition, these sets of dynamic descriptions and their larval correlates would provide the necessary data for a dynamic model of larval mortality.

Most of the work on the ecology of marine fish larvae has been laboratory studies on behavior and feeding ecology of the larvae produced by major offshore fish stocks. Little work has been done on the early life history of tropical reef fishes and many other inshore forms. Predation has received little attention in all species. Field studies on natural causes of mortality and variation of growth are just beginning, but the tools now exist for such work. If we are to identify the causes of natural mortality in the sea, the incidence of starvation and predation must be estimated over the spawning range of the species and at all life stages, and these losses compared with estimated rates of mortality. The vertical position of larvae in the sea in relation to their foods, predators, and time of day also needs to be considered in such an analysis.

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SOME ASPECTS OF THE LIFE HISTORY OF LABORATORY-REARED PACIFIC MACKEREL LARVAE (*SCOMBER JAPONICUS*)

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The early life history of Pacific mackerel (*Scomber japonicus*) is described using laboratory rearing studies and an examination of the stomach contents of sea-caught larvae (Hunter and Kimbrell, 1980). The incubation period for mackerel ranged from 33 h at 23°C to 117 h at 14°C. At hatching, larvae were 3.1 mm long and weighed 0.04 mg of which 50% was yolk. At 19°C, the first incidence of feeding occurred 46 h after hatching and by 60 h (age 2.5 days) all larvae were capable of feeding. At this time, larvae were 3.6 mm long, eyes were fully pigmented, and only 10% of the yolk remained. Starvation became irreversible if larvae were not fed before age 4.5 days. At age 5 days, larvae were still capable of feeding but were not able to capture enough prey to survive.

Growth of mackerel larvae is characterized by a relatively slow, almost linear trajectory over the first 10–15 days, when larvae reached 6–7 mm, followed by a rapid acceleration of growth through metamorphosis (15 mm). Growth rates ranged from 0.58 mm day^{-1} at 16.8°C to 0.92 mm day^{-1} at 22.1°C and had a Q_{10} of 3.0. Mackerel larvae had a relatively high metabolic rate: oxygen consumption of larvae in a Warburg apparatus was 6.1 $\mu\, 0_2$ mg dry wt^{-1} hr^{-1} at 18°C and 11.4 μl 0_2 mg dry wt^{-1} hr^{-1} at 22°C.

Cruising speeds of mackerel larvae increased from 1.3 body lengths sec^{-1} for first-feeding larvae to 3.8 body lengths sec^{-1} for fish at metamorphosis. At typical cruising speeds, 3–5 mm mackerel larvae swam with a high tail beat frequency (~30 beats sec^{-1}) and principally modulated tail beat amplitude to change swimming speed.

Larval mackerel fed on zooplankton by executing a high amplitude tail beat and engulfing with an open mouth. When they reached 8 mm, 50% became capable of feeding on other fish larvae; larvae were seized from the side and manipulated before ingestion. Cannibalism was common in rearing groups, but ceased as larvae approached metamorphosis and began to school.

The ability of mackerel larvae to capture prey by engulfing them with an open mouth was correlated with the width of the mouth. Fifty percent of the larvae were able to capture a prey when the width of the prey was 85% of the width of the mouth, and 95% were able to do so when they prey was 57% of the width of the mouth.

Food of mackerel larvae in the sea consisted chiefly of stages of copepods. The maximum width of foods eaten increased rapidly with larval length and was equivalent to the maximum width of the mouth; the minimum size of prey eaten increased much more slowly. The mean width of prey eaten was about 40% of the mouth width. The larger organisms, constituting half of the prey eaten, accounted for 85–90% of the total volume consumed.

In conclusion, mackerel larvae are fast swimming, metabolically active, and grow rapidly in the laboratory, reaching metamorphosis in 16–24 days. The maximum size of prey eaten increases rapidly with larval size, but in the sea many prey are eaten that are substantially below the maximum size mackerel larvae are capable of ingesting. These observations indicate that growth or survival in the sea may be limited by the availability of larger prey.

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EFFECTS OF SOLAR AND ARTIFICIAL ULTRAVIOLET-B RADIATION ON LARVAL NORTHERN ANCHOVY, *ENGRAULIS MORDAX**

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Abstract—Northern anchovy larvae were exposed to various amounts of both natural (global solar) and artificial (sunlamps filtered by cellulose triacetate) UV-B energy over a 12-day period. Dosage was determined on the basis of a weighting function for biological effectiveness. The action spectrum on which this biologically effective dose for anchovy mortality is based was developed using broad-band spectroscopy. These experiments indicated that biologically adverse conditions exist near the sea surface. Larvae exposed in shallow containers to global solar UV for 12 days suffered significant UV mortality from February to October. Larvae surviving all solar and artificial UV doses were smaller than those not exposed to UV. [Lowest dosage = 398 $\mathrm{J \cdot m^{-2}_{(bio.eff.)}}$.] Fifty percent of the larvae survived a cumulative dose of 605 $\mathrm{J \cdot m^{-2}_{(bio.eff.)}}$, or 50 $\mathrm{J \cdot m^{-2} \cdot day^{-1}_{(bio.eff.)}}$. Dose reciprocity did not hold; when a similar cumulative dose was given in the first 4 days of 12, there were about one-half as many survivors.

One meter below the sea surface the daily solar UV dose (corrected for average cloud cover) is equal to or greater than 50 $\mathrm{J \cdot m^{-2}_{(bio.eff.)}}$ (33 N, 118 W), the daily equivalent of the LD_{50}, for 7 months of the year (March to September) at moderate chlorophyll-a concentrations (0.5 $\mathrm{mg \cdot m^{-3}}$). These data suggest that larvae in the sea may be subject to some UV-B stress at present. Owing to their seasonality of spawning and vertical distribution, anchovy populations may not be gravely endangered by moderate degrees of stratospheric ozone diminution.

INTRODUCTION

Studies of over 60 aquatic microorganisms, protozoa, algae and small invertebrates indicate that most are sensitive to current levels of ultraviolet-B (UV-B) radiation incident upon the water surface (NAS, 1979)‡. More recent studies, better quantified, indicate that at doses comparable to daily levels of UV-B energy presently incident on the water surface, the growth of chain-forming diatoms is reduced (Thomson *et al*., 1979), as is the biomass and specific diversity of attached marine algae (Worrest *et al*., 1978) and survival of coral reef epifauna (Jokiel, 1980). Similarly, a UV-induced mortality of a marine pelagic copepod (Karanas *et al*., 1979) and pelagic crab and shrimp larvae (Damkaer *et al*., 1980) could occur at present UV-B levels. Hunter *et al*. (1979) examined the sensitivity of northern anchovy (*Engraulis mordax*) during the 4-day embryonic period (egg and yolk-sac stages) and found that brain and eye lesions as well as growth retardation could occur on larvae at or near the ocean surface if the ozone layer were reduced by 25%.

All of these investigations indicate that a high sensitivity to UV-B occurs in some small marine organisms, but the effect on natural populations of increased UV radiation due to ozone reduction remains unclear owing to technical uncertainties and lack of data. The technical uncertainties result from imperfect solar simulation in the laboratory. Problems include the use of artificial sources whose spectra differ greatly from natural solar radiation, the use of unrealistically high fluence rates, failure to establish whether photorepair mechanisms were fully activated in the laboratory, and the arbitrary use of UV action spectra to weight laboratory data with subsequent extrapolation therefrom to conditions in the sea. Assessment of the effects of UV on natural populations is difficult without data on the change in abundance of species with depth, the depth of penetration of UV in specific marine habitats, and appropriate weighting of the effects data by the seasonal abundance of the species of interest.

Our objective was to improve our previous estimates of UV effects on northern anchovy larvae by reducing some of these technical uncertainties, and to address the problem of assessment of UV effects of larval populations in the sea. Anchovy larvae needed to be tested to determine if the relation between cumulative dose and mortality shown in the 4-day experiments would hold for longer periods of exposure. In the sea, UV-B exposure effects might be

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‡*Abbreviations*: bio.eff., biologically effective; Chl *a*, chlorophyll *a*; CI, confidence interval; CTA, cellulose triacetate; LD_{50}, lethal dose to 50% of the organisms; NAS, National Academy of Sciences, USA; SL, standard length.

cumulative over as many as 23 days. [After about 23 days at 16°C, the anchovy swim bladder becomes functional and in daylight the larvae migrate vertically to depths beyond the reach of significant UV-B penetration (Hunter and Sanchez, 1976).]

In our past work larvae were tested under three different artificial UV-B spectral irradiance distributions, all substantially different from natural global solar irradiance. The energy from artificial sources was weighted by the DNA action spectrum of Setlow (1974) and the relation between the DNA-weighted dose and mortality was used to forecast effects in the sea under various ozone optical depths. This procedure remains open to question until the findings can be verified by experiments conducted under natural global solar irradiance. Consequently, our specific goals became: (1) to determine whether the same mortality in larval anchovy occurs when the total cumulative dose received in 4 days is, instead, spread over a longer period at lower fluence rates (12 days); (2) to test larvae under natural global solar radiation in order to verify the apparent UV-B sensitivity of anchovy larvae as well as the adequacy of the DNA weighting procedure; and (3) to make a preliminary estimate of the effect of ozone decrease on natural larval populations.

MATERIALS AND METHODS

Apparatus. Test containers were maintained under artificial UV-B in temperature-controlled water tables in the aquarium of the Southwest Fisheries Center and under global solar radiation on the roof of the Center. The containers were of opaque black plastic (36 cm in diam. and 17.5 cm deep) containing 10 *l* of filtered (2 μm) seawater and covered with a filter top. All treatments and controls consisted of 10 containers each. Banks of fluorescent lamps (Westinghouse FS-40 Sunlamps® for UV energy and General Electric Chroma 50® lamps for visible energy) were all aged for 400 h before use, and were suspended over the aquarium water tables in an aluminum foil-lined room. The aquarium system had a 12-h daily light–dark cycle with 7 h of UV radiation centered on the 12-h light period. The roof system used only natural solar energy.

Filters. Filter tops for test containers in the aquarium consisted of 0.13 mm thick pre-solarized cellulose triacetate (CTA) and 0.13 mm Mylar® plastic. The CTA eliminated UV-C energy from the sunlamps and brought the energy distribution closer to the solar UV spectrum; the Mylar® eliminated UV-B in control containers. (See Hunter *et al.*, 1979, for transmittance of these filters.)

In the solar experiments, 1–3 sheets of 0.13 mm thick Teflon® plastic were used to attenuate UV and visible radiation. One sheet of Teflon® transmitted 67%, two sheets 46%, and three sheets 38% of the incident UV radiation (integral from 290–380 nm), whereas the visible radiation (integral from 380–800 nm) was attenuated to 79, 55 and 48% for one, two, and three sheets of Teflon®, respectively. The ratio of transmitted UV (290–380 nm) to visible (380–800 nm) radiation was about 0.83. We do not believe that this minor change had a significant effect on the results of the solar experiments since the level of photorepair light was more than that needed in these experiments (Kaupp and Hunter, 1981).

The UV treatment containers had only Teflon® tops, but were accompanied by a set of containers having the same thickness of Teflon® and an additional sheet of Mylar®. This control group provided a measure of the combined effects of UV-A and visible radiation independent of UV-B effects. Another solar control had container tops which held three sheets (0.39 mm) of Teflon®, black screen cloth (53% transmission) and Mylar®; these filters in total transmitted only 6% of incident radiation (UV-A + visible radiation). This level of illumination approximated that for the aquarium control containers. Teflon® was used in all solar experiments because it diffused incident radiation. One sheet of Teflon® reduced the UV-B shadowing at the bottom of the containers to within 35% of peak irradiance under extreme sun conditions (clear sky and low sun angle).

Radiometry and the control of UV-B intensity. We varied the intensity of UV-B radiation in the aquarium system by covering the sunlamps with opaque aluminized Mylar® tape, changing the diameter of perforations in Mylar® sheets in the treatment container tops (Hunter *et al.*, 1979) and by adjusting the height of the lamp banks. Solar UV-B dosage was varied by changing the number of Teflon® sheets in the container tops, and by taking advantage of the natural variation in solar radiation.

In the aquarium, UV radiation was continuously recorded with a Norris UV-B radiometer (Optronics model 725) and in the solar system it was recorded continuously with a UV-B radiometer and a Robertson–Berger meter (Berger, 1976). Visible energy was measured continuously in the solar system with a deck cell illuminometer. At intervals during an experiment, measurements were made with a spectroradiometer (Optronics Model 741-V) which was calibrated against a radiometric standard traceable to the National Bureau of Standards. The spectral irradiance measurements were used to convert the continuous records of the radiometers to dosage. For additional details of the apparatus, filters, and radiometry see Hunter *et al.* (1979).

Experimental design. At noon, about 1.5 days after spawning, 100 anchovy eggs were stocked in each test container; eggs hatched about 24 h later (larval age 0 day). The yolk-sac-stage ended 5 days after hatching (larval age 4 days) and feeding began. From age 3–5 days, larvae were fed the dinoflagellate, *Gymnodinium splendens*, maintained at a density of 100–200 cells/m*l* and from age 5–12 days the rotifer, *Brachionus plicatilis*, maintained at a density of 10–30 *Brachionus*/m*l* (Lasker *et al.*, 1970; Hunter, 1976). Experiments ended at age 12 days: at this time larvae had experienced 12 daily UV exposures. In the aquarium system total cumulative exposure was about 82 h, but in the solar experiments total hours of exposure and dosage varied seasonally and with cloud cover. At the end of each experiment, the surviving larvae were counted and preserved for subsequent length measurements and histological analysis. The survival in treatment containers was normalized to that of the companion control by dividing the number of survivors in a treatment by the number surviving in the control (Table 1), and a dose-response line was calculated for the normalized data using probit analysis (Finney, 1952).

RESULTS

Action spectrum

The relationship between UV-B dose (unweighted) and survival for a 12-day exposure to global solar UV differed by two orders of magnitude from that under artificial UV radiation in the aquarium (Fig. 2). The LD_{50} dose for solar UV, in the integral from 290–320 nm, was 1060 $kJ \cdot m^{-2}$ (95% CI, 871–1280 $kJ \cdot m^{-2}$), whereas that for artificial UV-B, in the integral from 285–320 nm, was 11.0 $kJ \cdot m^{-2}$ (95% CI, 10.1–11.8 $kJ \cdot m^{-2}$). Thus interpretation of all

Table 1. Cumulative UV-B dose and survival for anchovy larvae exposed 12 days to artificial and solar UV-B

Date	Dose $Jm^{-2}_{bio.eff.}$	Mean number of survivors[1]		Percent survival normalized to control
		$\bar{X}$	SD	
Artificial UV-B[2]				
25.05.78	0	48.2	15.9	100.0
	1109	10.3	8.5	22.9
	1522	0.5	0.8	1.0
07.06.78	0	55.8	30.6	100.0
	726	28.3	16.9	47.9
	1336	0.1	0.3	0.2
22.06.78	0	71.5	21.1	100.0
	517	58.0	26.9	81.1
	679	33.2	10.7	46.4
11.07.78	0	70.0	11.3	100.0
	587	47.3	21.0	67.6
	788	24.1	7.5	34.4
06.09.78	0	49.4	15.3	100.0
	559	31.3	7.4	63.4
	777	1.9	1.7	3.8
28.06.79[3]	0	31.7	14.8	100.0
	642	9.9	6.3	26.7
Solar UV-B[4]				
05.10.78	0	38.3	17.3	100.0
	1505	1.0	1.6	2.6
15.02.79	0	44.8	7.8	100.0
	385	23.3	11.5	51.8
23.02.79	0	17.8	8.4	100.0
	1277	0.2	0.6	1.1
20.03.79	0	36.9	13.3	100.0
	630	14.6	5.4	39.6
19.04.79	0	10.2	7.0	100.0
	662	2.0	3.4	19.6
03.05.79	0	60.0	12.7	100.0
	569	46.2	14.3	77.0
17.05.79	0	47.6	10.6	100.0
	599	21.9	18.8	46.0
01.06.79	0	51.6	18.1	100.0
	606	31.1	12.3	60.3
14.06.79	0	25.7	14.1	100.0
	669	23.1	14.9	89.9
28.06.79	0	33.6	21.4	100.0
	753	12.0	12.8	35.7
12.07.79	0	21.1	10.6	100.0
	697	14.2	8.9	67.3
26.07.79	0	39.6	12.0	100.0
	1098	3.8	3.5	9.6
16.08.79	0	14.8	9.1	100.0
	1005	0.8	1.1	5.4
30.08.79	0	23.9	12.3	100.0
	975	1.2	2.1	5.0
13.09.79	0	16.8	17.6	100.0
	873	2.8	3.3	16.7
21.09.79	0	39.6	21.8	100.0
	544	19.1	13.4	48.2
	790	10.9	7.5	27.5
12.10.79	0	31.4	12.2	100.0
	539	4.7	4.6	15.0
25.10.79	0	67.0	10.1	100.0
	398	42.0	10.0	62.7

[1] Stocking density was 100 eggs per container, and means are for 10 containers.

[2] To approximate unweighted Jm^{-2} over 285–320 nm, multiply by 18.2

[3] This dose was given in the first 4 days of the experiment, i.e. eggs, 0-, 1- and 2-day-old larvae.

[4] To approximate unweighted Jm^{-2} over 290–320 nm, multiply by 1750.

results pivots on the choice of an appropriate action spectrum for weighting UV-B effects. Hunter *et al.* (1979) weighted their dose-response data (4-day exposure) by the DNA action spectrum of Setlow (1974) using the analytical fit of Green and Miller (1975), and brought along common line dose-response data for three different artificial UV-B spectra. When we used the same technique to equate effects under solar and artificial UV for a 12-day exposure, the data clearly did not converge. The LD_{50} for a 12-day exposure to artificial UV-B when weighted by the Green and Miller equation underestimated effects under solar UV-B by 66%.

We re-examined the action spectrum of Green and Miller (1975) and derived an action spectrum that would converge the 12-day exposure data for artificial and solar UV-B doses. This action spectrum gives more weight to wavelengths greater than 300 nm relative to the Green and Miller fit to the Setlow DNA action spectrum. The greatest difference occurs at 320 nm, where approximately a tenfold difference exists (Fig. 1b). This change in the form of the action spectrum greatly affected the weighting of the solar data (increase of 66%), but had little effect on data for artificial UV sources (reduction of less than 3%). Thus, use of our action spectrum did not alter the relation among the three weighted UV dose-response curves for a 4-day exposure (Hunter *et al.*, 1979), because all three were based on modifications of the spectral irradiance from FS-40 Sunlamps®. This action spectrum is an adequate weighting function for solar, as well as for three different artificial spectra. Henceforth in this paper, we use this action spectrum to weight all dosages.

Our action spectrum for anchovy mortality and that for DNA damage presented by Setlow (1974) (and modeled by Green and Miller, 1975) is within the 95% confidence intervals of the data used for determination of action spectra for the killing of phage, bacteria, and several vertebrate cell lines (depicted in Fig. 1b). Our broad band spectroscopy has a variance larger than that associated with the data presented for comparison. Our action spectrum cannot be statistically separated from the Green and Miller fit to the data of Setlow (1974), but we will refer to our weighting as 'biologically effective' (i.e. bio. eff.). Our weighted dose can be converted to an approximate unweighted dose using coefficients in Table 1. Representative spectral irradiance distributions for artificial and solar sources are given in Fig. 1. The spectrum of solar UV radiation varied continuously in our experiments, but the conversion is adequate for making rough comparisons with other studies.

Survival

Fifty per cent of anchovy larvae (12-day solar and aquarium experiments combined) survived a cumulative dose of $605\ J \cdot m^{-2}_{bio.eff.}$ (95% CI = 541–676 $J \cdot m^{-2}_{bio.eff.}$) or a mean daily dose of $50\ J \cdot m^{-2}_{bio.eff.}$. This daily dose is within the range of daily UV fluence we have measured in La Jolla, California over the last 2 years of daily monitoring. On clear days, it has ranged from 25 $\mathrm{J \cdot m^{-2}_{bio.eff.}}$ in December to 215 $\mathrm{J \cdot m^{-2}_{bio.eff.}}$ in July. These data indicate that biologically adverse conditions exist near the sea surface at present ozone concentrations. There is no reason to doubt this conclusion since larvae suffered significant mortality from February through October when exposed in shallow containers to the La Jolla sun for 12 days. In all solar experiments, larvae were exposed to levels less than the actual solar radiation because the containers were always covered with Teflon® which attenuated UV-B as well as the energy at other wavelengths (see the Methods section for the degree of attenuation).

The cumulative UV dose required for 50% mortality in 12 days (605 $\mathrm{J \cdot m^{-2}_{bio.eff.}}$) was about half that required for the same mortality in 4 days (1195 $\mathrm{J \cdot m^{-2}_{bio.eff.}}$) (Hunter *et al.*, 1979). The 12-day experiments gave a more sensitive assay of UV damage. To survive past yolk absorption (age 4 days), larvae must be able to search and capture live prey, whereas in the 4-day experiments, larvae needed only to metabolize yolk. It seems unlikely that the severely

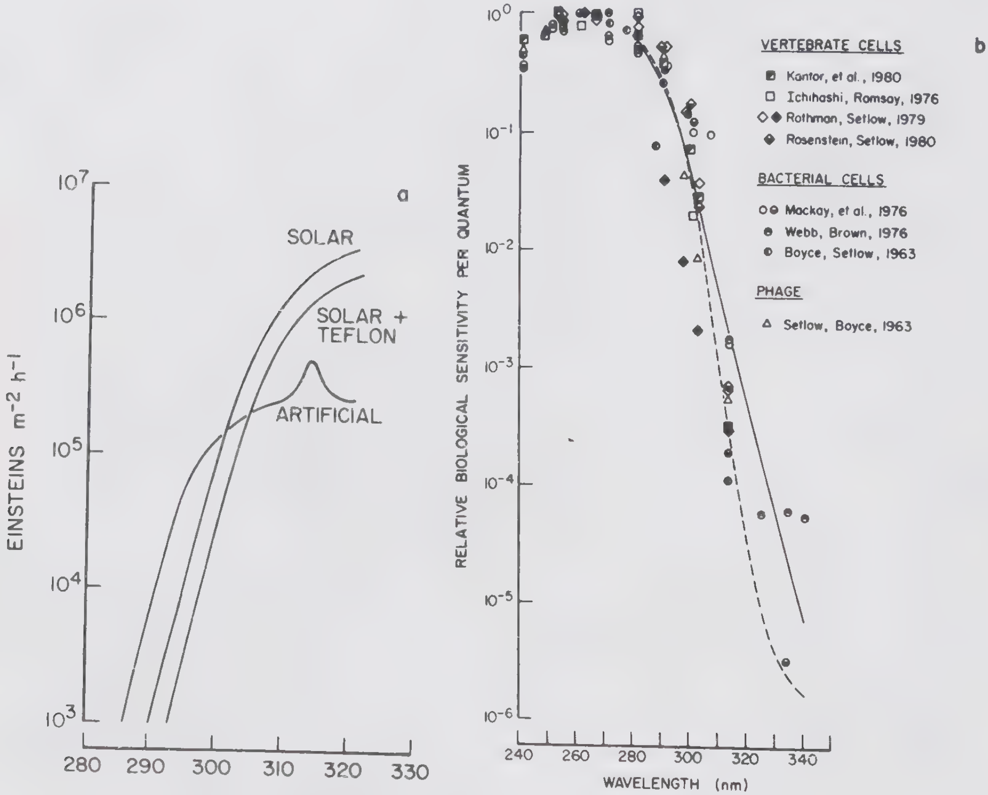

Figure 1. (a) Comparison of solar and artificial UV-B spectra. The solar spectra, measured at local apparent noon, 5 March 1979 (32.5° N, La Jolla, CA), is shown with and without attenuation produced by 0.13 mm of Teflon®. The unattenuated solar spectrum represents 37.8 $\mathrm{J \cdot m^{-2}_{bio.eff}}$ and 25.4 $\mathrm{J \cdot m^{-2}_{bio.eff.}}$ attenuated. The artificial spectrum (used in the laboratory experiments) was produced by Westinghouse FS40 Sunlamps® filtered by 0.13 mm of cellulose triacetate and represents 37.4 $\mathrm{J \cdot m^{-2}_{bio.eff}}$. (b) Comparison of DNA action spectrum with data for the killing of vertebrate and bacterial cells, and inactivation of a phage; (---), Green and Miller (1975) fit to the DNA action spectrum of Setlow (1974); (——), empirical action spectrum used to weight dose-response data for anchovy; and points from UV action spectra in literature normalized to the wavelength yielding the maximum response in the particular study. Points for vertebrate cells include: unscheduled DNA synthesis (Ichihashi and Ramsay, 1976; for 10 $\mathrm{J \cdot m^{-2}}$ dose) (□), and inactivation (Kantor *et al.*, 1980; average values for normal and DNA exision-repair deficient strains) (◩) of human fibroblast; DNA pyrimidine dimer formation (◇) and killing (◆) of Chinese hamster cells (Rothman and Setlow, 1979); and the killing of haploid frog cells (Rosenstein and Setlow, 1980; average of data with and without photoreactivating light) (⬙). For bacterial cells: killing of *Salmonella typhimurium* (rec A) (○), and *E. coli* (rec A) (◒) (Mackay *et al.*, 1976; average of stationary phase and exponentially growing cells); stationary phase *E. coli* (B/r and B/r Hcr) (◓) (Webb and Brown, 1976); of *E. coli* (15 TAU) (◐) (Boyce and Setlow, 1963). For the inactivation of phage T_4B (△) (Boyce and Setlow, 1963).

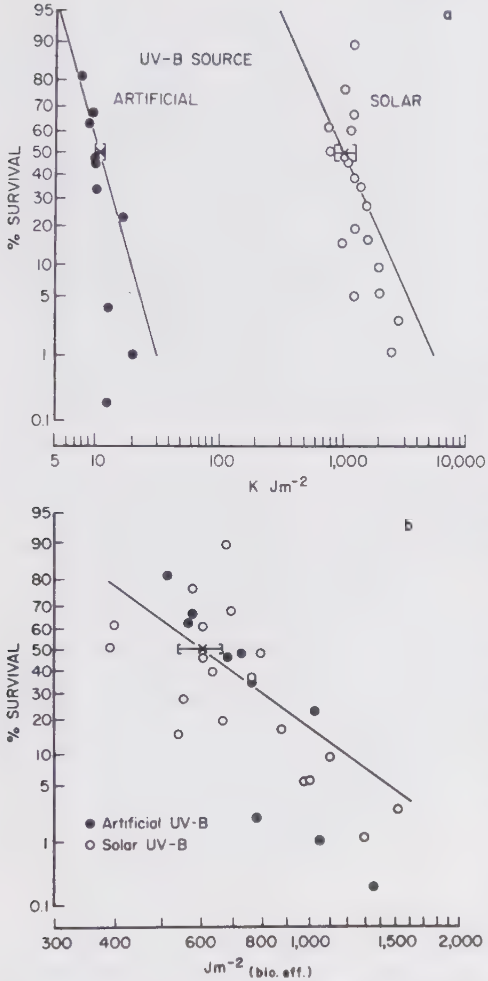

Figure 2. (a) Relation between unweighted UV-B dose ($\mathrm{kJ \cdot m^{-2}}$; 285–320 nm) cummulated over 12 days and survival of larval anchovy exposed to artificial (●) and solar (○) radiation. The lines represent the regression of survival probit (Y) on $\log_{10}$ dose (X) where $Y = 4.962\ X - 15.04$ for artificial source, and $Y = 3.467\ X - 1594$ for solar source. Bars and crosses indicate $\mathrm{LD}_{50} \pm 95\%$ confidence intervals. (b) Relation between weighted UV-B dose (285–320 nm) cummulated over 12 days for both artificial and solar exposures. The regression of survival probit (Y) on log dose (X) where $Y = 4.275\ X - 6.89$.

damaged larvae that survived the high dosages used in the 4-day experiments (high incidence of eye and brain lesions) could ever feed successfully.

More importantly, dose reciprocity did not hold. In a single aquarium experiment (28.6.79), we exposed eggs and larvae in 10 containers for 4 days to a cumulative dose of $642\ \mathrm{J \cdot m^{-2}_{bio.eff.}}$ which is close to the LD_{50} dose for 12 days. Only 26.7% (95% CI, 14.4–39.0%) of these larvae survived by age 12 days. Thus only half the expected number of larvae survived when an LD_{50} dose for 12 days was given at a high dose rate for 4 days. Dose rate, as well as, cumulative dose appear to be important variables. This fact does not alter the interpretation of our dose-response relationships, since we administered dosages over periods comparable to the daily solar cycle or used the actual natural pattern of daily global solar radiation.

We also tested for combined effects of solar UV-A and visible radiation on survival of larvae. Solar energy at wavelengths 315 nm or greater did not show a statistically significant effect on survival after 12 daily exposures. A slight mortality from solar energy above 315 nm may exist, since survival in those groups that received no UV-B was slightly lower than (but statistically inseparable from) control groups maintained under filters that transmitted only 6% of radiation above 315 nm and no UV-B. If real, this effect is probably negligible in the sea.

The extent of photorepair of UV-induced damage could be a significant variable in the interpretation of survival of UV-B radiation. That this is an insignificant factor in the present study is shown by Kaupp and Hunter (1981). They found that the level of photorepair fluence in our laboratory apparatus was sufficient to fully stimulate photorepair of UV damage in anchovy larvae, while the solar photorepair fluence was many times that of the required level.

Growth

Larvae surviving 12 daily exposures to UV-B in the aquarium and in the solar experiments were smaller than survivors in the controls. Significant differences existed ($P = 0.05$) even at the lowest dosages ($517\ \mathrm{J \cdot m^{-2}_{bio.eff.}}$ in aquarium experiments; $398\ \mathrm{J \cdot m^{-2}_{bio.eff.}}$, in solar experiments). The mean standard length of larvae at age 12 days decreased as a linear function of dosage in the aquarium experiments (Fig. 3). Regression analysis for the solar data was inappropriate because water temperature, which has a marked effect on growth, could not be rigorously controlled.

Temperatures varied only ±0.2°C over the course of the aquarium experiments but fluctuations of 2–3°C were not uncommon in the solar experiments and the mean temperatures in the latter ranged from 14.3–16.1°C, whereas the means of aquarium experiments were 16.0 ± 0.2 C. Regardless of the temperature problems, the decline in average larval length with dosage followed about the same pattern in both groups of experiments. This analysis indicates that growth was inhibited by exposure to UV-B and the magnitude of the effect was a linear function of dosage. Retardation of growth could translate into additional mortality if survival were to be assessed after the 12th day of life.

PRELIMINARY ASSESSMENT OF EFFECTS OF UV-B ON LARVAL POPULATIONS

Realistic assessment of the effects of UV-B on the anchovy larval populations requires knowledge of

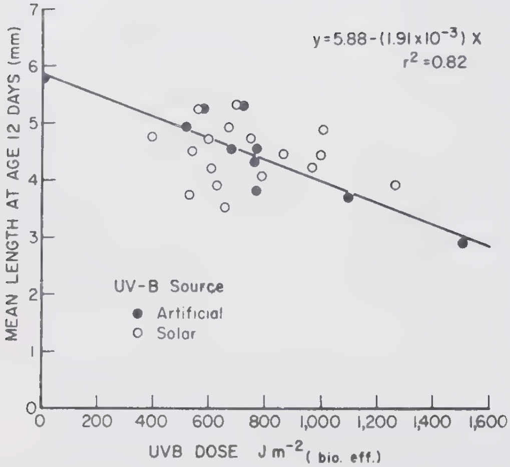

Figure 3. Relation between mean standard length of anchovy larvae (preserved in 4% formaldehyde) after 12 daily exposures of UV-B as a function of cumulative weighted UV-B dose. Regression line is fit only to data from artificial UV-B sources (●).

seasonal changes in larval abundance, incident UV-B, spatial and temporal variation in the depth of penetration of UV-B in the habitat, vertical distribution of larvae in the sea, rates of vertical mixing of eggs and larvae, and natural rates of mortality for eggs and larvae. At present, many of these parameters can only be approximated or are unknown. Nevertheless, a preliminary assessment is useful because it may be a long time before these parameters for natural populations are accurately estimated and because such calculations identify the dominant factors in the analysis.

In this calculation we assume that no vertical mixing of eggs and larvae exists. There are no data on the vertical mixing of fish larvae, though the possibility certainly exists. It is important to recognize that our assumption of a static vertical distribution (without vertical mixing) presents the most extreme case of potential UV damage. Vertical migration and mixing could greatly reduce our estimate of the effect of UV radiation.

Hunter and Sanchez (1976) investigated the possibility that anchovy larvae vertically migrate. Using the original data of Ahlstrom (1959), they compared day and night catches of larvae less than 11.75 mm (standard length, SL) to those equal to or greater than 11.75 mm (Ahlstrom did not give larval length in his paper, and his original data must be used to make the calculation). Hunter and Sanchez (1976) found evidence for a diel change in depth distribution in larvae greater than 11.75 mm, but no evidence for a diel change in depth distribution in larvae less than

Table 2. Proportion of northern anchovy larval population affected by UV-B radiation at present (0.32 cm) and at 25% reduction (0.24 cm) in ozone concentration

	0.32 cm Ozone (ambient)				0.24 cm Ozone (25% reduction)			
			Larvae at or above LD_{50}[3]				Larvae at or above LD_{50}	
Months	Daily fluence UV-B ($J \cdot m^{-2}_{bio.eff.}$)[1]	Depth of LD_{50}[2] (m)	Percent[4]	Percent weighted by relative larval abundance[5]	Daily fluence UV-B ($J \cdot m^{-2}_{bio.eff.}$)[1]	Depth of LD_{50}[2] (m)	Percent	Percent weighted by relative larval abundance
J	25	0	0	0	40	0	0	0
F	52	0.11	3.76	0.62	82	1.34	13.32	2.17
M	94	1.74	15.09	2.53	149	2.95	19.65	3.29
A	150	3.03	19.90	3.96	238	4.21	23.48	4.67
M	158	3.17	20.37	2.70	250	4.35	23.85	3.16
J	167	3.32	20.85	1.65	265	4.50	24.28	1.92
J	162	3.24	20.59	1.16	257	4.42	24.06	1.36
A	147	2.97	19.72	0.37	233	4.16	23.32	0.44
S	111	2.20	16.96	0.30	176	3.40	21.09	0.37
O	65	0.72	9.73	0.11	103	1.95	15.98	0.18
N	30	0	0	0	48	0	0	0
D	20	0	0	0	32	0	0	0
Σx				13.40				17.56

[1] The sea surface irradiance is taken from Baker *et al.* (1980) coefficients for the model of Green *et al.* (1974) for 33°N, and adjusted for 18-yr average cloud cover (1961 1978) for the Los Angeles Bight (30–35 N, 115–120°W, Renner, 1979) using the equation of Bener (1964) and then weighted by an empirical fit to the DNA action spectrum.

[2] Depth in sea where the daily UV-B fluence is equivalent to the LD_{50}. The depth of UV-B penetration was calculated for moderately productive water (0.5 mg Chl *a* m^{-3}) using the downwelling irradiance diffuse attenuation coefficients of Baker and Smith (personal communication); $K_T = 0.3630$ for 0.32 cm ozone and $K_T = 0.3702$ for 0.24 cm ozone.

[3] $50 \; J \cdot m^{-2}_{bio\,eff}$.

[4] The monthly percent of larvae at or above the LD_{50} depth was calculated using the vertical distribution data for northern anchovy larvae (< 11.75 mm standard length; Hunter and Sanchez, 1976) of Ahlstrom (1959) adjusted to unit sea surface (Smith and Richardson, 1977) and fitted by the equation, $y = 11.44 \, x^{0.5}$, $r^2 = 0.99$, for the data from the surface to 28 m, where y is the cumulative percent of larvae from the surface to depth x, in meters.

[5] 10-year average larval abundance from Lasker and Smith (1977) was used to weight the percent of larvae affected by UV-B for each month; see Fig. 2.

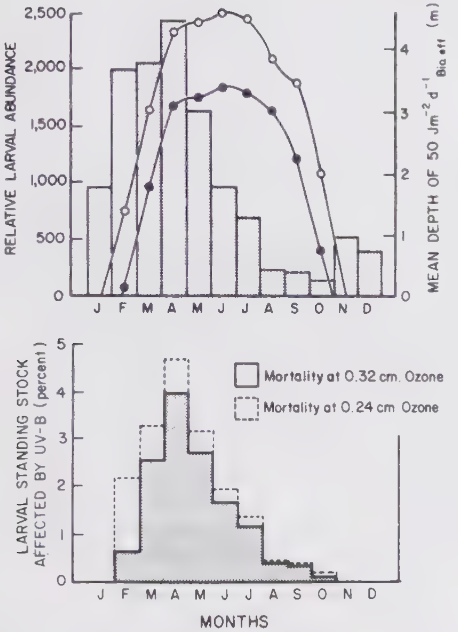

Figure 4. (a) Relative abundance of larval anchovy per month (bars) and mean depth of daily UV-B penetration of 50 J $\cdot$ $m^{-2}_{bio\cdot eff.}$ in the sea per month at present (●) and at 25% reduction in ozone (○). 50 J $\cdot$ $m^{-2}_{bio\cdot eff.}$ is the daily equivalent of the LD_{50} for anchovy larvae cumulated over 12 days. Data sources are given in footnotes to Table 1. (b) Percent of annual larval anchovy standing stock affected by UV-B (50 J $\cdot$ $m^{-2} \cdot d^{-1}_{bio\cdot eff.}$) per month at present ozone concentration [0.32 cm optical ozone depth (——)] and at 25% reduction in ozone [0.24 cm optical ozone depth (---)] according to calculations given in Table 1.

11.75 mm. As the maximum size of larvae at the end of our experiments was 6.5 mm SL, we used Ahlstrom's data for larvae less than 11.75 mm SL to calculate the vertical distribution, using techniques outlined by Smith and Richardson (1977). Smaller larvae may migrate vertically but the change in their vertical distribution is not detectable using Ahlstrom's original data. The equation fitted to Ahlstrom's data, and other documentation for these calculations, are given as footnotes in Table 2. We assume that larvae of the size considered here (SL $\leq$ 6.5 mm) do not migrate vertically and have a depth distribution similar to that given in Table 2.

We also assume that all larvae at those depths with UV energies equal to the LD_{50} (50 J $\cdot$ $m^{-2} \cdot day^{-1}_{bio.eff.}$) will die, while those receiving lesser dosages will survive. This criterion was chosen because of the symmetry of the dose-response curves about the LD_{50} value. It does not take into account sublethal damage, nor the fact that UV-B radiation decreases with depth faster than does the anchovy larval abundance. This use of the LD_{50} limits the conclusions from the calculation of effects of enhanced UV-B to an indexing of effect. These effects will alter the absolute value of our index of mortality, but they will have little or no effect on the rate of change of the index in response to ozone depletion.

Estimates of daily UV-B energy entering the sea were derived from Baker *et al.* (1980) adjusted for average cloud cover using the equation of Bener (1964). Average cloud cover data were 18-yr monthly means (Renner, 1979) for an area in the Southern California Bight (30–35°N, 115–120°W), which is the center of the anchovy spawning region (Ahlstrom, 1967). To estimate the depth of penetration of UV-B in the sea at various ozone concentrations, we used the equations and the attenuation coefficients of Smith and Baker (1979) for moderately productive ocean water (0.5 mg Chl *a* m^{-3}) weighted by our action spectrum for anchovy mortality. This chlorophyll concentration is typical of the Southern California Bight during the spawning season (Owen and Sanchez, 1974).

The proportion of larvae in the water column affected by UV-B (proportion of larvae at or above the depth where the daily UV-B dose = 50 J $\cdot$ $m^{-2}_{bio.eff.}$) is highest in June (21% at 0.32 cm ozone; 24% at 0.24 cm ozone) and declines with the seasonal changes in UV radiation (Fig. 4; Table 2). Although the predicted rate of UV mortality is highest in June, the abundance of anchovy larvae (shaded area, Fig. 4, upper) is relatively low (Lasker and Smith, 1977). When the loss rate per month at present ozone levels is weighted by the monthly larval abundance, the months that contribute most to the total annual UV mortality are March, April and May (Fig. 4, lower). The principal effect of a 25% reduction of ozone is to advance the period of UV vulnerability one month in the spawning season; the period of vulnerability would thus begin in February instead of March and remain at elevated levels through the peak months of spawning.

Our calculations indicate that at the present time about 13% of the annual production of larvae could be lost because of UV-B mortality and this may increase to about 18% at a 25% reduction in ozone (Table 2). The increase in the estimated UV-B mortality for the larval population is nearly a linear function of ozone concentration with mortality increasing about 0.2% for each percentage decrease in ozone (Fig. 5). Thus ozone decline produced only a minor increase in predicted UV-B mortality for the population, but a loss of 13% of larval standing stock at present ozone levels seems high. If such a UV-B mortality exists, it may have little effect on the population because natural rates of mortality from other causes are high; the rates decline from about 53% per day for eggs (Smith and Lasker, 1978) to about 17% per day for 12-day-old anchovy larvae (Zweifel and Smith, 1981).

The estimated effect of ozone diminution on larval anchovy populations is low for several reasons. Each year UV radiation increases during the peak months of spawning (January–April) at a rate equivalent to about a 25% reduction in ozone every month

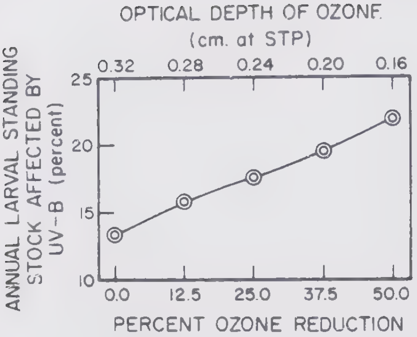

Figure 5. Estimated annual loss of larval anchovy standing stock (%) as a function of optical depth of ozone. The method of calculation is illustrated in Table 1.

(Table 2). This condition (decreasing spawning during increasing UV-B) reduces the relative impact of ozone loss in our calculations. Impact is also reduced because anchovy larvae exist below depths where significant UV effects occur as well as within such depths. A 25% reduction in ozone in moderately productive waters (0.5 Chl a m^{-3}) is equivalent to about a 1 m increase in the depth of penetration of the biologically effective dose. This increase in depth of penetration does not have a major effect on populations that are distributed over many meters of depth.

Some factors could completely change our assessment, viz.: an extreme change in the form of the vertical distribution of larvae, or seasonal changes in larval vertical distribution; seasonal changes in UV-B diffuse attenuation coefficients in the habitat; elevated UV sensitivity at a specific life stage of the larvae; or vertical mixing or movement of the larvae. These considerations suggest that the life history traits that would greatly increase vulnerability of a marine planktonic organism to ozone decline are: (1) the entire population is confined to a very limited depth range—perhaps a few meters—so that an increase in the depth of UV-B penetration of 1 m or less could have important consequences; or, (2) the period of vulnerability is confined to a short span in the spring or winter (about 1 month at our latitude), or to the summer months so that adaptation to UV is limited to a relatively constant fluence rate.

Our estimate of the effects of ozone diminution on larval anchovy standing stocks is patently simplistic, having many uncertainties and assumptions, and should therefore be regarded only as an index of the possible losses due to enhanced UV-B radiation. The final estimated loss to the annual standing stock is an index of effects, and should not be confounded with actual mortality rates, which are size-specific. Despite these shortcomings we believe the analysis demonstrates that ozone loss of 25% or less may not have a great effect on the larval anchovy population, at least in the first 12 days of life. The possible effects of sublethal radiative doses in the eventual survival and reproductive ability of anchovies has yet to be investigated.

DISCUSSION

An important ecological implication of this research is that UV radiation is probably a major factor in the early life history of many pelagic marine fish larvae. The important life history characteristic of the northern anchovy is the restriction of intense spawning to periods of low UV radiation. Fish larvae that exist only at the surface during the months of most intense UV radiation probably have evolved mechanisms to cope with high fluence rates. Such larvae are often deeply pigmented (H. G. Moser, unpublished manuscript, NMFS, Southwest Fisheries Center, La Jolla, CA) or may have other protective mechanisms, seemingly, as does the Pacific mackerel which spawns intensively in June, has little apparent pigmentation, but is much more resistant to UV radiation than are anchovy (Hunter *et al.*, 1979). Obviously, the vertical distribution of larvae and their vertical migration are also important adaptations.

High sensitivity to UV radiation may be a common trait among many pelagic clupeoid fish worldwide. The period of maximum spawning in many of the major stocks of clupeoid fish does not coincide with the period of maximum UV-B fluence (Table 3). Clupeoids that spawn very near shore or in bays, e.g. *Herengula jaguana* and *Opisthonema oglium* (Table 3) do not follow this pattern, but such species seldom form large fish stocks. Such inshore species could be as sensitive to UV-B radiation as northern anchovy because the inshore and bay habitat may provide protection from UV radiation owing to high Chl concentrations and turbid conditions of such shallow waters. Inshore areas and bays in southern California typically have Chl concentrations as high as 5 mg Chl a m^{-3} (Brewer *et al.*, 1980). This value is very high relative to the one used in our calculations, 0.5 mg Chl a m^{-3}, which is representative of offshore areas. Such a difference in Chl concentration would reduce the depth of penetration of a biologically effective dose by a factor of about 5.

We do not wish to imply a direct cause and effect relationship between seasonality of spawning and UV-B fluence. Spawning seasons probably evolved to coincide with optimum larval feeding conditions and not to avoid UV-B radiation. That spawning intensity is low when UV-B intensity is the highest in many clupeoids indicates that they may be less resistant to UV-B radiation than other fish that spawn during high UV-B fluences at the same latitude. Our calculations for northern anchovy might apply to many of the world's clupeoid stocks that spawn pelagic eggs, because they show similar spawning patterns in relation to the annual UV cycle. Our present analysis indicates that these stocks may be subject to some UV stress today, but owing to their spawning season, vertical distribution, and high natural rate of mor-

Table 3. Relation between seasonal UV-B maxima and spawning maxima in various clupeoid fish

Species/location	Years of data collection	Latitude of sampling	Months winter north J	F	M	A	M	summer J	J	A	S	O	N	winter D	Portion of annual equatorial UV-B$_{DNA,eff}$	Source
			south J	A	S	O	N	D	J	F	M	A	M	J		
Engraulidae																
Engraulis mordax Southern California and Baja California	1951 60	32 N						UV[1]							0.50	Ahlstrom, 1967
					eggs and larvae[2] (66%)											
Engraulis capensis South Africa	1978–79	21 S						UV							0.78	Butterworth, 1979
						eggs (78%)										
Engraulis ringens Peru	1966–74	6–14 S					UV			UV					0.92	Santander and Castillo, 1976
					eggs (47%)					eggs (20%)						
Cetengraulis mysticetus Gulf of Panama	1956 57	9 N					UV			UV					0.92	Simpson, 1959
													eggs (99%)			
Clupeidae																
Brevoortia tyrannus Atlantic coast of USA	1965-66	34–41 N								UV					0.40	Kendall and Reintjes, 1973
												eggs (70%)				
Sardinops melanosticta Southern Japan	1949-51	35 N						UV							0.45	Nakai and Hattori, 1962
						eggs (79%)										
Sardenella anchovia Gulf coast of Florida	1971-74	24 30 N						UV							0.60	Houde *et al.*, 1979
												eggs (70%)				
Etremus teres Gulf coast of Florida	1971-74	24–30 N						UV							0.60	Houde *et al.*, 1979
			eggs (88%)													
Herengula jaguana Gulf coast of Florida	1971-74	24–30 N						UV							0.60	Houde *et al.*, 1979
								eggs (97%)								
Opisthonema oglinum Gulf coast of Florida	1971–74	24 30 N						UV							0.60	Houde *et al.*, 1979
								eggs (90%)								

[1] The line represents the months spanned by the most intense half of the annual UV-B flux for the given latitude.

[2] The spawning "season" (dashed line) was taken from net tow data cited in the reference given on the right-hand column. The percentage given refers to the portion of annual production represented by the spawning "season".

tality, they may not be greatly affected by ozone diminution. For the northern anchovy this seems to be the most tenable conclusion.

To confirm our assessment of UV effects on anchovy larval populations would require: better data on vertical distribution of larvae in the sea; measurement of seasonal pattern of Chl concentration (to estimate penetration of UV in the habitat); laboratory studies on the relative resistance to UV-B of various life stages of larval anchovy; and studies of the long-term effects of short-term exposure to UV-B radiation.

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CHAPTER 3

ECONOMIC ANALYSIS FOR NORTHERN ANCHOVY MANAGEMENT

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Published in July of 1978, the Pacific Fishery Management Council's management plan for the northern anchovy fishery off of California was the second plan (after salmon) to be implemented on the West Coast. The high priority given to the development of the anchovy plan was due largely to the apparent ecological importance of the fish stock and to the great political sensitivity of anchovy management issues in California. For the most part, traditional economic issues were drowned out by the noneconomic concerns of recreationists and public agencies. Nevertheless, a moderate amount of economic information was assembled and analyzed for inclusion in the plan that was eventually adopted. After the introduction of the planned regulations in September 1978, the economists and biologists responsible for most of the analysis at the National Marine Fisheries Service Southwest Fisheries Center continued to examine management strategies and issues pertinent to the northern anchovy. Most of the ideas, data, and analytical results presented in this paper resulted from the joint efforts of the management planning team at the Southwest Fisheries Center.[1]

This chapter is organized into four major sections. In the first section, five important economic issues are listed and described. Following that, a section is devoted to the presentation of biological, institutional and economic information providing a necessary real-world context for the management problems. In the third section economic theories are tailored to the specific needs of anchovy management, and analytical results are presented. In applying economics to the fishery, areas of theoretical weakness and data deficiency are revealed. In the concluding section the strengths and weaknesses of the existing economic analyses are reviewed, and recommendations for further research are advanced.

ECONOMIC ISSUES FOR ANCHOVY FISHERY MANAGEMENT

While no short list of topics can fully represent the complex management issues at stake in the formulation of public regulations for northern anchovies, the following five points cover the most substantial areas for economic analysis:

1. evaluation of the aggregate harvest rate by the U.S. fishery;
2. allocation of the fish harvest among various end uses;
3. analysis of the optimum investment in harvesting and processing capacity;
4. formulation of regulatory mechanisms to achieve the desired objectives for catch, investment and so forth; and
5. design of management information and monitoring programs.

To analyze any of these issues one must adopt some criterion or objective for management. A single economic objective that will provide the framework for the following discussions is the traditional one of maximizing the economic value of goods produced, net of production costs. Within this objective is contained the requirement that the fishery achieve productive efficiency, the minimization of costs incurred in producing the desired level of output. Within this context the careful identification of costs and values is clearly a principal task. Since neither the fish stock nor the recreationally caught fish are traded in markets, the economic analysis must account for nonmarketed and unpriced goods as well as commercial product values. As any student of welfare economics knows, the adoption of this "net economic yield" criterion for management cannot be rigorously defended since the distribution of income will be influenced by the fishery policy and we have not determined what changes in income distribution are desirable. Bromley and Bishop [1977] examine this aspect in great detail, concluding that the traditional approach to fisheries economics by focusing on economic efficiency issues ignores income distributional impacts and much of economic welfare theory. Assuming that any income distributional consequences of anchovy management decisions are on a small scale and that these can be remedied by other means, however, the traditional efficiency objective will serve as a useful guide in the following discussion.

Much of the economic theory of fisheries is devoted to the first topic listed above–evaluation of aggregate harvest rates. Since many extensive reviews of this theory are available [Anderson 1977; Clark 1976; and Peterson and Fisher 1977], no lengthy theoretical treatise is called for here. In application, however, the theory leaves much to be desired. As noted by Peterson and

Fisher, the "functional forms are too simple and their empirical content too low." Institutional, geographical and organizational content is often sacrificed to preserve mathematical tractability or to allow two-dimensional, pedagogical diagrams. Since we are addressing an actual management problem, simplicity-destroying complications must be introduced in some fashion. Three apparently important complications arising in the anchovy fishery are (1) the multipurpose nature of the fishing fleet; (2) the stochastic variability of the stock; and (3) the importance of anchovies as forage. Economic implications of these are discussed below.

Allocation among end uses, the second topic, is an important consideration for anchovy management because the widespread use of anchovies for live bait by both recreational and commercial fishermen is politically and economically more significant than their use as meal and oil. Market values per unit weight for live bait are estimated to be 8-10 times the value of fish used by reduction plants. One might be tempted to assume, therefore, that the free market forces could be counted on to assure the proper allocation to live bait, reduction fish and other end uses. This is not the case, however, because the two products are produced by two separate groups of fishermen having different equipment, locations and alternative opportunities. Most importantly, there is no institutional framework within which the live-bait interests can bargain with the reduction fishery interests to assure that the reduction fishery does not take all the available fish. In part this is a problem caused by the existing management procedures. An annual quota is set in the fall, while the major live-bait market occurs in the summer months. If the quota is taken before the summer begins, live bait would not be available at the appropriate time. Thus a set of separate quotas, or some other allocative device, is needed.

The third issue has occupied fishery economists concerned with the problem of "overcapitalization." Under some regulatory schemes, the fishery may be induced to harvest the proper quantity of fish (by some definition) but private, profit-oriented fishermen will have strong incentives to construct and operate far more fishing vessels than necessary to take the allowable catch. Arbitrary limits on some inputs to the production function encourages greater (and uneconomic) use of other inputs. This breach of the productive efficiency criterion is especially likely when regulations rely on "standards" (like quotas, size limits and gear restrictions) rather than incentive-compatible mechanisms (like taxes and property rights) to achieve narrowly defined harvest goals. A public policy toward fishery inputs, however, must rely on a normative theory of optimum input use, especially the optimum level of capital investment. An important secondary issue is whether the expected extra cost associated with unregulated input use exceeds the benefits of regulation.

The fourth issue listed above is concerned primarily with the economic efficiency of the management operations once the specific objectives of management have been defined. Experience with regulatory programs elsewhere, especially in pollution control and environment regulation, has led most economists to recommend pricing mechanisms rather than absolute standards as regulatory tools. Others prefer property right arrangements. But as Scott [1979] points out, either system can achieve a given set of goals regarding efficiency, equity and conservation. One of the principal considerations in choice of regulatory tools must be the prospective cost (economic and political) of gathering and monitoring the data needed to assure that the regulations are being obeyed with sufficient regularity to support the management program. This issue has not received the extensive formal analysis that it deserves in the fisheries literature. The cost of running a successful management program with a given set of regulations probably depends crucially on the extent to which the rules incite individual fishermen to evade enforcement and monitoring efforts. And these incentives will depend on the physical ease with which rules can be broken without detection, as well as upon the financial consequences of rule-breaking behavior.

The final issue I have suggested for economic examination requires that the tools of economics be turned inward on the analysts themselves. One frequently hears that more economic data, better stock assessments and more extensive enforcement of regulations are "needed." These claims are sometimes motivated by requirements laid down in the Fishery Conservation and Management Act (FCMA), such as National Standard (2) (Sec. 301) calling for the use of the "best scientific information available," or the "optimum yield" definition [Sec. 3(18)] which requires the consideration of economic and social factors. But information is costly to obtain. Thus optimum yield cannot logically call for vast reservoirs of data which contribute little to the decision-making process. Similarly, "best" scientific information is not necessarily the most comprehensive or conclusive information, but rather the most appropriate level of knowledge, given cost and time constraints. The economic theory of information suggests that new data be valued by the expected increase in discounted future returns associated with the decisions dependent on that information. (See, for example, Hirshleifer and Riley [1979].) This opens up a relatively unexplored area for analysis in fisheries management, but one which could potentially contribute significantly to the efficiency of management operations.

There are undoubtedly fruitful areas for economic analysis in addition to the five discussed here. But these five seem sufficiently important to the management of northern anchovies to demand immediate attention. As implied in much of the earlier discussion, the author considers it to be crucial that economic analysis be guided by the biological, economic and institutional context in which the managed industry exists. To adequately understand the relative importance of various policy issues and to intelligently judge the adequacy of economic analyses, therefore, the reader must have a firm grasp of the situation faced by fishery managers in California. Consequently, the next section of the paper is devoted to a presentation of pertinent background information.

THE BIOLOGICAL, INSTITUTIONAL AND ECONOMIC CONTEXT

Biological Basis

Important characteristics of the fish stock include location, size, potential yield and function in the ecosystem. The following summary information on these characteristics for the anchovy stock is drawn from Huppert et al. [1980a] which is a slightly modified version of the Anchovy Fishery Management Plan [1978], and Huppert et al. [1980b], an updated investigation of the population dynamics model and other technical issues. These two reports rely upon the many scientific studies carried out by the California State Department of Fish and Game (CF&G), the National Marine Fisheries Service, Scripps Institution of Oceanography and California Academy of Sciences. The brief review contained below serves to place the discussion of fishery management in context, but is not a substitute for the more extended treatments available elsewhere.

The northern anchovy, *Engraulis mordax*, is a small, pelagic schooling fish occurring along the west coast of North America from Queen Charlotte Sound in the north to the southern tip of Baja California. Significant physical differences in the fish found within this range suggest the existence of three separate subpopulations [Vrooman and Paloma 1975]. As shown in Figure 1, the northern subpopulation occurs essentially north of San Francisco; the central subpopulation extends from San Francisco to Punta Baja; and the southern subpopulation stretches south from Punta Baja to the tip of the Baja California peninsula. The central subpopulation is the most abundant of the three, and it is the stock unit adopted for management by the Pacific Fishery Management Council (PFMC). The bulk of the population biomass is consistently located in the Southern California Bight, an area of approximately 20,000 square nautical miles bounded by Point Conception, California in the north and by Ensenada, Mexico in the south.

Estimates of the central subpopulation's spawning biomass (Table I) are based on anchovy larva abundance estimates derived from the ichthyoplankton collections of the California Cooperative Oceanic Fisheries Investigations (CalCOFI), a consortium of scientific research agencies involved in oceanographic research. The biomass estimates for the 1951-1966 period suggest a logistic-shaped growth path. After reaching a peak biomass of 4.7 million

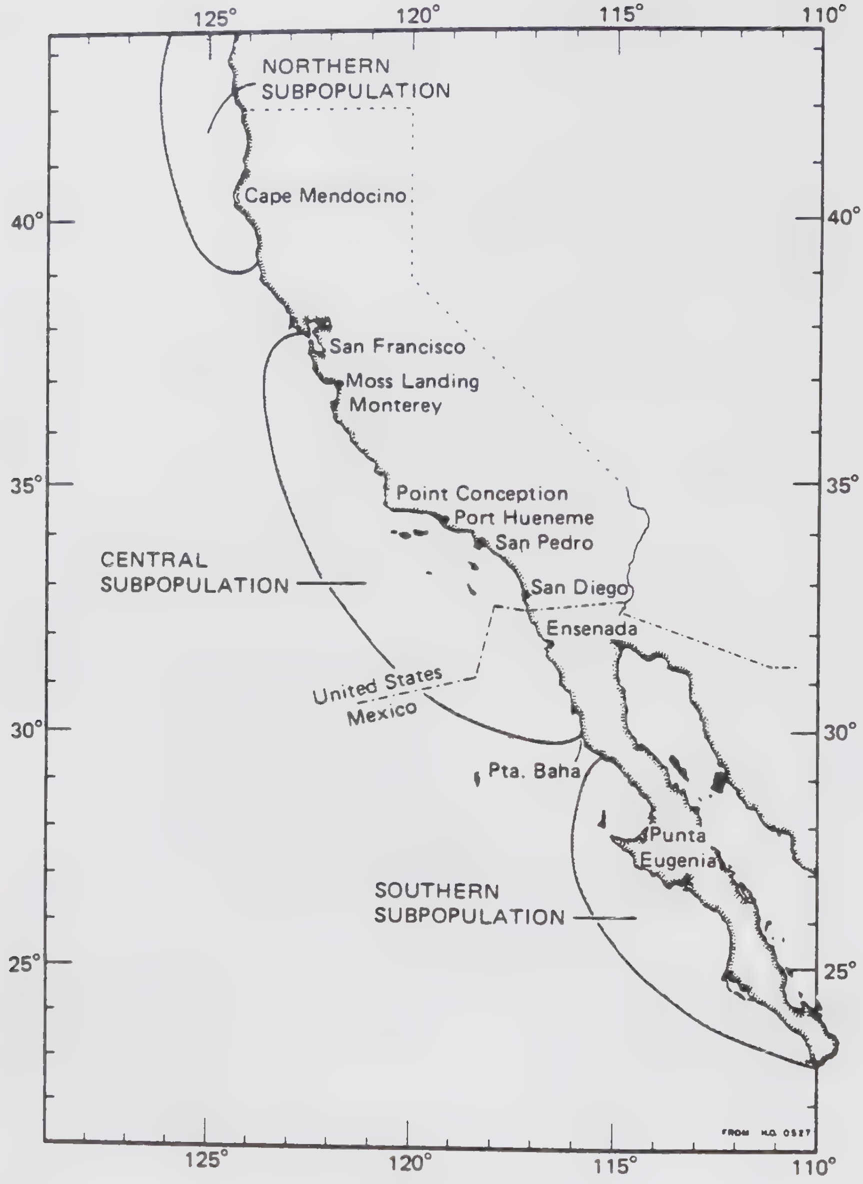

Figure 1. Approximate location of three subpopulations of northern anchovy.

Table I. Population Size and Harvests from the Central Subpopulation of Northern Anchovies (in thousands of short tons)[a]

Year	Estimated[b] Biomass	California Landings		Ensenada Landings[c]
		Commercial	Live-bait	
1951	180	3	5	–
1952	156	28	7	–
1953	510	43	6	–
1954	768	21	5	–
1955	845	22	6	–
1956	485	28	6	–
1957	1167	20	4	–
1958	1479	6	4	–
1959	1514	4	5	–
1960	1540	3	5	–
1961	1159	4	6	–
1962	2989	1	6	–
1963	4254	2	4	–
1964	2901	3	5	–
1965	4659	3	6	10
1966	3572	31	7	15
1967	–	35	5	25
1968	–	16	7	17
1969	2999	68	5	4
1970	–	96	6	6
1971	–	45	6	4
1972	2784	69	6	7
1973	–	133	6	2
1974	–	83	6	48
1975	3603	159	5	61
1976	–	122	5	79
1977	–	110	5	157
1978	1304	11	5	143
1979	1723	52[d]	5[d]	208[d]
1980	1775	–	–	–

[a] Sources: California Department of Fish and Game and Instituto Nacional de Pesca.

[b] After 1966 the ichthyoplankton cruises upon which the biomass estimates depend were reduced from annual to tri-annual; in 1979 annual survey were resumed.

[c] Data not available for Ensenada before 1965.

[d] Preliminary estimates.

short tons in 1965, however, the stock has fluctuated and declined sharply. The 1978 biomass of 1.3 million tons was the smallest anchovy stock encountered since 1961. In addition to the spawning biomass measured by the larva census estimate, there is a substantial biomass of juvenile fish. In view of the rapid growth in juvenile anchovies, the cohort of immature fish probably reaches a maximum biomass slightly before the end of its first year of life. The fish mature between their first and second years, and the recruiting yearclass of fish begins to appear in the commercial catch a few months before it reaches one year of age. Thus the fishery could exploit a stock larger than the estimated spawning stock in the absence of any minimum size regulations to protect juveniles.

Although there was a small anchovy fishery for canning in the early 1950s, the fluctuations in biomass prior to the inception of the California reduction fishery in 1966 were due primarily to natural causes.[2] Additional evidence of natural fluctuations in stock size is provided by the anaerobic sediment data from Soutar and Isaacs [1974]. Smith [1978] converted the scale depositions in the sediment samples into biomass estimates for 38 five-year intervals from 1775 to 1970. The average anchovy biomass over this period is estimated to be 4.5 million metric tons with a coefficient of variation equal to 0.47.[3] This degree of variability is consistent with that observed in clupeoid fish stocks around the world [Murphy 1977].

The central subpopulation also undergoes north-south shifts. Stauffer [1978], again using CalCOFI larva census data, found that the percent of the standing stock of anchovy larvae north of the United States/Mexico boundary varied between 45 and 86% during the 1951-1975 period. Over the whole period combined 70% of the larvae were found in U.S. waters. Assuming that larva distribution is a good indicator of fish distribution, the data suggest that 70% of the fishable stock is within the United States jurisdiction.[4]

Published studies of the potential yield from the central subpopulation are based on a variety of population models and result in a disturbingly wide range of biological yield estimates. The most optimistic estimate was that of MacCall et al. [1976]. Using a crude, rule-of-thumb method suggested by Gulland [1970], MacCall et al. concluded that the potential yield of northern anchovy is over 2 million tons.[5] A cautionary note following the estimate suggested that this level of yield would not be sustainable due to the year-to-year fluctuations in the stock.

Radovich and MacCall [1979][6] presented a model based on the assumption that the stock observed during 1951-1975 followed a logistic growth equation. The estimated model is:

$$B(t) = B_{max}/[1 + e^{-r(t - t_0)}] \qquad (1)$$

where B_{max} = 4.0 million tons

r = 0.36

t_o = the time at which the inflection in the growth curve occurs

The stock growth rate is given by the time derivative of the logistic equation. A maximum to the growth rate occurs at $B_{max}/2$ where dB/dt = 360,000 tons/yr. To calculate the potential yield from a fishery Radovich and MacCall assumed that the biomass measurement represents the spring spawning stock just after the new cohort of fish recruits to the spawning stock, and that the fishery takes fish from the stock at a steady rate during the year. Since the maximum annual growth represents the change in stock size at year-end, and the fishing mortality competes with natural mortality during the year, a fishery should be able to take more than the annual growth in equilibrium. Estimating that the excess of potential yield over potential growth at about 25%, Radovich and MacCall estimate MSY to be 450,000 short ton/yr.

In developing the yield estimates for the Anchovy FMP, MacCall modified his population model somewhat. The main innovation was the explicit treatment given to the size of and yield from the recruiting yearclass. Also, the logistic equation was reestimated after adjusting for the levels of harvest taken in California. The most recent estimates for the parameter of the logistic equation are $B_{max} = 4.207 \times 10^6$ short tons and $r = 0.3638$ (see Huppert et al. [1980b]). A reparameterization allows the population transition equation to be written as:

$$B_{t+1} = B_t K/(H + B_t) \tag{2}$$

where $K = B_{max}/(1 - e^{-r}) = 13.8 \times 10^6$ tons

$H = Ke^{-r} = 9.6 \times 10^6$ tons

The population transition equation applies to an unfished population.

Noting that the rate of natural mortality is due primarily to predation, starvation and other factors not related to the fishery, we assume that the percentage rate of mortality to the spawning biomass is constant. Since both somatic growth and mortality in numbers of fish occur simultaneously, we use a net mortality rate, (M-G), equal to 0.8 (see MacCall [1980]). If the measured spawning biomass disappears at this rate during a calendar year between biomass measurements, then any excess of biomass over adult fish survival appearing in accordance with Equation 2 must be recruitment. Thus recruitment can be expressed as a function of the previous year's biomass as follows:

$$R_{t+1} = B_t K/(H + B_t) - B_t c^{-(M-G)} \tag{3}$$

In the presence of a fishery which causes a constant percentage rate of mortality, denoted F, the population transition equation becomes:

$$B_{t+1} = B_t K/(H + B_t) - B_t c^{-(M-G)}(1 - e^{-F}) \tag{4}$$

where it is assumed that the juveniles are unaffected by the fishing. The catch taken during a year can be expressed as the following function of B_t and F:

$$Y_t = (F/F + M - G)\,(1 - e^{-(F + M - G)})B_t \tag{5}$$

Figure 2 depicts the equilibrium annual stock growth and the equilibrium yield curve given the parameter estimates noted above.

To examine the effects of harvesting juveniles Equations 3 to 5 must be modified to account for fishing mortality on juveniles. This involves specifying the relative availability of juveniles to the fishing effort. In MacCall [1978] and Huppert et al. [1980a,b] the juveniles are estimated to be available for 20% of the year with about 76% of the catchability of adults. Since the insertion of the juvenile harvest complicates the algebra while introducing no useful insight into the model, the interested reader is referred to the abovementioned reports. The only important aspect of the harvest of juveniles is its impact on the equilibrium yield curve. As juveniles become more vulnerable the equilibrium yield from the fish stock falls as shown in Figure 2.

Another way of viewing the population dynamics shows the mortality of adults and recruitment to the stock as two separate components. In Figure 3, for example, the biomass at time T generates the recruitment at time T + 1 through the function labeled A. This recruitment function is just the graph of Equation 3, and the straight line out of the origin labeled "replacement" represents the total loss of adult biomass due to natural causes in a year. If the size of recruitment equals the total mortality, the population just maintains itself; hence the term "replacement." For spawning biomasses below the equilibrium level of 4.2 million tons, the recruitment exceeds the replacement level and net growth occurs. Two important issues regarding the validity of the estimated population model can be discussed with the aid of this figure. First, the estimated stock-recruitment relationship is not a very close "fit" to the 15 observations shown on the diagram, but the null hypothesis that recruitment is unrelated to spawning stock size can be rejected with better than 95% confidence.[7] Thus the statistically fitted equation can be used to make conditional predictions, but with a high degree of uncertainty. The standard deviation of the error about the recruitment function for the 15 observations

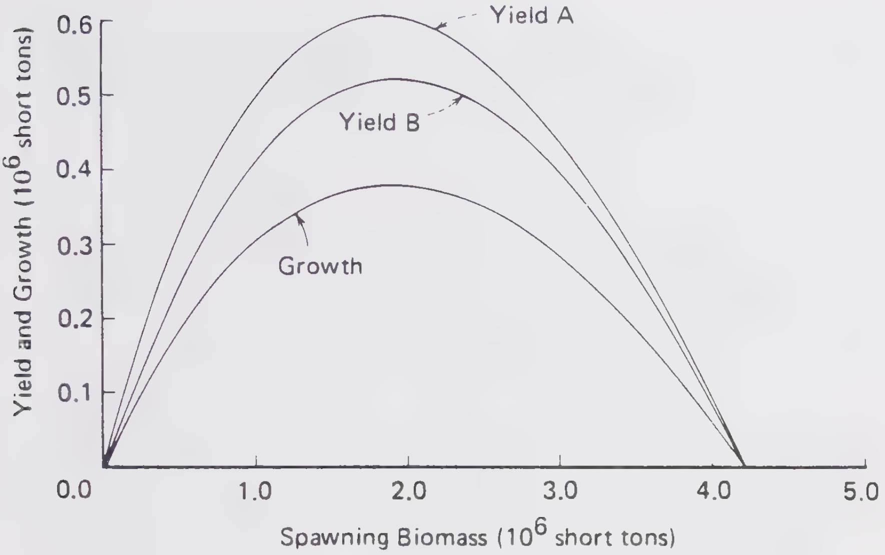

Figure 2. Population growth and yield curves for the northern anchovy, central subpopulation, with (Yield A) and without (Yield B) harvest of immature fish.

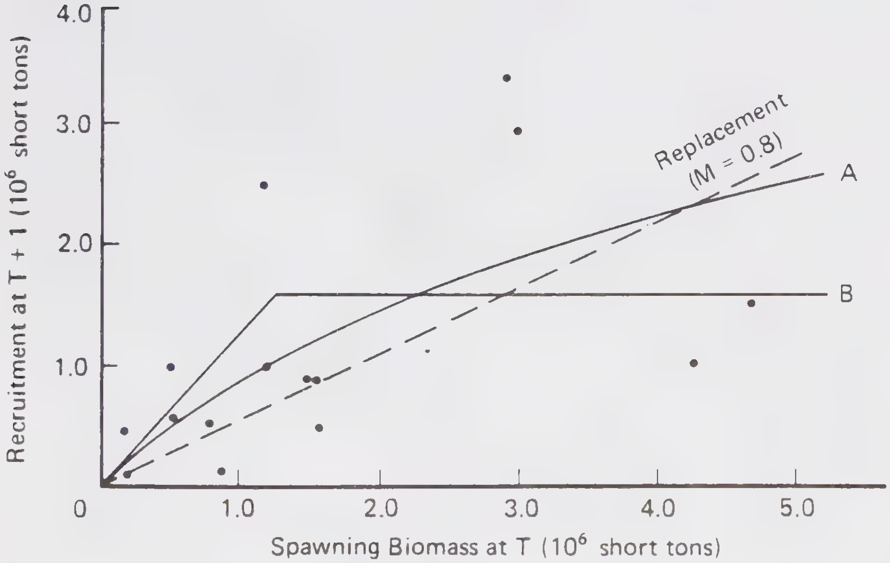

Figure 3. Alternative stock-recruitment models. Model A is the logistic model, and Model B is the modified constant Recruitment Model.

is about 860,000 tons. Second, an alternative model of recruitment, which is labeled B in Figure 3 assumes that recruitment equals 1.247 times spawning biomass up to a biomass of 1.225 million tons and equals 1.527 million tons for larger stock sizes. This alternative model cannot be distinguished statistically from the original logistic-based model with a reasonable degree of confidence.[8] Given these two facts, the approach to management of the anchovy fishery must somehow recognize the level of uncertainty in the population model. One method described below is to adopt a stochastic decision-making framework.

One immediate consequence of the stochastic recruitment and yield curves is that the concept of sustainable yield is inapplicable. Although the peak of the yield curve may occur at 520,000 tons, this level of yield is in no sense sustainable. An attempt to take this "MSY" year after year can be expected to severely deplete the population within a short period of time. Although the theory of managing stochastic, fluctuating fish populations is not very well developed, the few published papers seem to support some general conclusions. Beddington and May [1977], for example, conclude that populations fluctuating due to environmental conditions will become unstable under either constant fishing effort or constant catch policies. They conclude that a feedback control policy should be adopted.

All the above comments address anchovy management solely in terms of the fish catch and the dynamics of the stock. But anchovies, like most clupeoid fishes, are a forage stock for many predators. In the California Current some of the known predators are commercially and recreationally important fish. These include tunas, barracuda, sea basses, jack mackerel, Pacific mackerel, Pacific bonito, yellowtail, striped bass, salmon, swordfish, striped marlin and others. Other known or suspected predators of northern anchovy include marine mammals (common dolphins, northern fur seals, California sea lions and others), and many varieties of marine birds including the brown pelican, a designated endangered species.

Anchovies are, of course, just one of a group of small schooling fish species that are preyed on by larger fish, birds and mammals. Other species are sardine, saury, mackerel, herring and lanternfish. In her "biomass budget" for the California Current Region, Green [1978] estimated that the total predation on small schooling fish amounts to at least 24 million ton/yr. Of this total estimated consumption of small fish only a small portion could be contributed by the anchovy stock.[9]

Management policies for anchovies should take into consideration the effect of reduced anchovy stocks on the food supply for, and resultant average stock size of predator species. But the available information is rather sparse and inconclusive regarding these interspecies impacts. Some predators may be much more dependent on the availability of anchovies than would be suggested by an examination of average food intake. For instance, there may be a short, but critical mating or spawning season during which the need for anchovy schools is essential. Comprehensive research may someday provide reliable, predictive models to reveal these ecosystem linkages. But current knowledge simply lacks the detail necessary to contribute quantitative models to the fishery management process.

Political/Institutional Setting

Management of the anchovy reduction fishery in California must, as Kaneen [1977] remarked, "walk in the shadow of the sardine fishery." Two legacies of the now-defunct sardine fishery play a significant role. First, the obvious failure of state authorities to prevent catastrophe in the sardine fishery, despite intense and lengthy scientific study, bolstered the mistrust of fisheries managers by recreational fishing and environmental groups. California sardines supported the United States' largest (by tonnage) fishery during the mid-1930s and early 1940s. The peak catch of 791,000 tons occurred in 1936-1937, and the average annual catch during 1934-1946 was 600,000 tons. A severe drop in stock size occurred in the late 1940s, followed by a moderate rebound in 1950-1951, and another collapse in 1952. After many years of small landings, sardine harvests were prohibited entirely in 1970. Years of scientific research resulted in some detailed post mortems [Murphy 1966; Ahlstrom and Radovich 1970], but the causes for the stock collapse are still not fully understood. Perhaps the most common view, as expressed by Murphy [1966; 1967; 1977], is that the fishery was extracting sardines faster than could be sustained during the 1940s until the recruitment of two successive poor year classes (1949 and 1950) reduced the stock to a size too small to generate large year classes. There is still controversy over the annual yield that the sardine population could have sustained (see Murphy, [1966] and MacCall, [1979]).

A second legacy from the sardine days is the institutionalized bias against the reduction of fish into meal and oil. Early in the sardine fishery the state legislature was persuaded to regulate the reduction fishery (without, of course, putting effective restraints on the fishing for canneries). Interested readers are directed to Schaefer et al. [1951] for a detailed account of these regulatory actions. The important fact is that producers, who had begun to pass a larger fraction of the fish through reduction plants, were prevented from utilizing the fish in the way they found most profitable. Mandel [1975] notes that this constituted a specific rejection of economic profit as a criterion for determining the best use of California resources. Clearly, this was not the only or most prominent rejection of simple economic criteria for resource allocation.

When the state legislature transferred control of the anchovy reduction fishery to the California Fish and Game Commission in 1965, it was largely motivated by the sharp and politically unrewarding controversy between commercial interests and recreational groups. Strengthening the commercial fishermen's argument for a reduction fishery was the scientific recommendation that a 200,000-ton experimental quota be established for anchovies. The CalCOFI committee had reasoned that the vastly expanded anchovy stock might be retarding the reestablishment of the more valuable sardine (see CalCOFI [1966]). A 200,000-ton catch was reckoned to be about 10% of the standing stock, a minimum withdrawal necessary to produce a measurable change in the anchovy/sardine system. The commission established an annual quota of 75,000 tons for the 1965-1966 season and maintained the quota until 1970 when the fishery expanded enough to justify larger quotas. The U.S. fishery has yet to reach a catch total of 200,000 tons.

Because of its ancestry, therefore, California's anchovy management program has had an undeniably conservative slant. Whether this is justifiable or not depends largely on subjective judgment. A sympathetic evaluation would emphasize the risk inherent in an aggressive fishery. Undetected failures of recruitment, combined with heavy fishing could easily lead to the demise of another fish stock. One suspects that rugged commercial fishermen, and perhaps society-at-large, would be willing to accept these risks in a simple commercial venture. The remaining unquantified factor, however, is the potential impact on other fish stocks and the subsequent deleterious effect on marine recreational and commercial fishing activities. As noted in the previous section of the paper, multispecies and ecosystem models are as yet unable to provide practical advice on these issues, and the possibility exists that some delicate balances in the system might be tipped inadvertently by a more extensive anchovy fishery.

Mexico's attitude toward the development of a reduction fishery for anchovies is spawned in a different environment. Establishment of income-generating fisheries is a key component in Mexico's national plan for marine resources. The Food and Agriculture Organization of the United Nations (FAO) assisted Mexico in developing plans for fishery development specific to the northern anchovy off of Baja California. Wadsworth [1974] outlined a plan for an eventual 500,000 ton/yr. fishery with 200,000 tons being produced at Ensenada and 100,000 tons at each of three more southerly ports. A later report [FAO-Mexico 1978] repeats the earlier plan and specifically mentions the fact that California does not intend to exploit its portion of the anchovy stock.

Mexico's plan for fishery development is reaching fruition through the efforts of Pesquera Zapata S.A. de C.V., a company jointly held by Mexican investors and Zapata Corporation of the United States. This new venture established a reduction plant in Ensenada and brought in six new U.S.-built purse seine vessels. Initial operations in 1976 were followed by rapid growth of the fishery to about 150,000 ton/yr. in 1977 and 1978 (see Table I). The Mexican fishery evidently takes some unknown fraction of its fish from the southern subpopulation, but most undoubtedly comes from the central subpopulation. Because of the rapid diffusion of fish throughout their range, it can be expected that withdrawals to the south of the international border will affect the average abundance of anchovies to the north. Thus the need for some reconciliation of goal and procedures is clear. To date the United States government has been unable to induce Mexican officials to seriously consider a joint fishery management regime.

Economic Characteristics

The three main segments of the anchovy fishing fleet are (1) the so-called "wetfish" fleet in southern California[10]; (2) a smaller group of vessels in Monterey Bay; and (3) the live-bait fishing vessels scattered along the southern California coast in ports with substantial amounts of marine recreational fishing. All of these vessels use roundhaul nets, with the purse seine type predominating in the commercial reduction fishery and the lampara type being commonly used for live-bait fishing. Many of the wetfish vessels are survivors of the sardine fishery, but some are small tuna purse seiners and one is newly constructed specifically for the anchovy/mackerel fishery. As indicated in Table I, nearly all the anchovy catch is for the reduction processors. The U.S. reduction harvests are distributed geographically with 80% of the catch landed in Los Angeles, 16% in Port Hueneme and 4% in Monterey.

The number of vessels landing anchovies varies considerably from year to year. In 1975, the peak year for U.S. reduction fishery landings, 80 vessels participated, while only 29 reported landing anchovies for reduction during the 1979-1980 fishing season. Many of the vessels capable of fishing extensively for anchovies shift to the mackerel fishery (jack and Pacific mackerel) for substantial portions of the year and fish opportunistically for Pacific bonito, bluefin tuna and squid. Table II shows that anchovy landings generally account for the bulk of the wetfish landings by weight. But due to the lower prices received for anchovy (about $42 vs $160/ton for mackerel in 1980), the revenue derived from anchovy fishing is less than half of the total revenue for the fleet.

Live-bait operations generally consist of at least one roundhaul vessel and some bait receivers for holding the fish in good condition. Currently, there are 11 or 12 such live-bait operations. A major portion of the typical live-bait dealer's business is covered by contract obligations to local partyboat and charter boat businesses. Gruen, Gruen and Associates [1979] estimated the 1977 live-bait sales to be worth $2.6 million. Aggregate estimated live-bait landings have remained consistently between 500,000 and 700,000 tons over the past 10 years.

Although a wide range of vessel sizes and catch rates is exhibited in the anchovy reduction fishery, existing data are sufficient only to support a

Table II. Landings and Values of Wetfish Fleet in San Pedro and Port Hueneme, 1960-1979[a]

				Landings (short tons)					
Year	Anchovy[b] (Reduction)	Jack Mackerel[c]	Pacific Mackerel[c]	Pacific Bonito[d]	Bluefin Tuna[e]	Pacific Sardine[f]	Squid[g]	Total	Deflated Value[i]
1960	–	36.338	18.279	603	1,488	27.185	163	84.056	–
1961	–	46.968	22.011	4,199	2,553	21.006	3,299	100,036	–
1962	–	43.963	24.265	975	4,702	6,386	1,855	82,146	–
1963	–	46.895	20.109	1,964	4,441	2.895	2,337	78,641	–
1964	–	43.554	13,411	1,236	2,602	10,043	3,530	74,376	–
1965	171	31,957	3,517	2,729	1,881	792	4,695	45.742	–
1966	19.009	19.806	2.290	8,748	3,140	425	3,736	57,154	–
1967	23.952	18.623	571	7,714	1,528	70	3,799	56,257	–
1968	9,518	27,354	1,564	7,423	1,921	51	4,781	52.612	–
1969	62,390	25,736	1,173	6,340	2,008	41	4,256	101,944	–
1970	91.892	23,615	309	4,292	691	134	7,305	128,238	–
1971	42,288	29,854	77	4,684	1,211	82	2,598	80,794	–
1972	65,843	25,495	53	7,708	2,525	163	2,288	104,075	–
1973	126,082	10,016	27	9,203	1,911	66	1,278	148,583	–
1974	75,420	12,709	66	6,801	2,157	7	2,910	100,070	–
1975	148,516	18,370	142	1,680	3,796	3	4,350	176,857	–
1976	118,463	22,380	173	1,922	2,013	8	3,015	147,974	–
1977	101,402	52,288	3,650	1,334	868	2	4,709	164,253	–
1978	10,898	34,000	12,282	800	1,424	1	3,307	62,712	–
1979	48,545	17,575	29,503	250	1,597	17	2,260	99,747	–
				Ex Vessel Value ($1000)					
1960	–	1,534.1	751.1	34.9	362.7	1,117.7	7.6	3,808.1	9,177.5
1961	–	1,952.7	1,182.6	214.2	661.7	1,108.7	102.2	5,222.1	12,475.6
1962	–	1,826.3	1,024.9	55.6	1,320.7	408.7	46.5	4,682.7	10,985.6
1963	–	1,954.5	860.0	108.6	1,000.7	235.1	61.6	4,220.5	9,757.8
1964	–	2,048.2	666.2	60.3	633.1	456.2	86.0	3,950.0	8,990.2
1965	5.9	1,753.5	222.7	141.3	491.5	89.7	101.0	2,805.6	6,248.1
1966	388.2	1,377.9	185.8	694.5	920.9	147.0	104.1	3,818.4	8,232.4
1967	484.4	1,411.5	71.3	646.4	373.7	28.4	124.9	3,140.6	6,576.4
1968	167.0	2,085.4	167.3	616.2	584.3	14.5	142.8	3,777.5	7,570.1
1969	1,224.2	1,949.9	121.2	588.4	641.1	9.2	153.4	4,687.4	8,943.7
1970	2,030.1	1,860.6	49.1	609.3	258.4	57.7	291.6	5,156.8	9,344.0
1971	999.8	2,408.9	7.2	845.9	504.0	35.2	85.5	4,886.5	8,424.1
1972	1,566.0	2,147.6	6.0	1,403.5	1,086.7	48.9	81.9	6,340.6	10,493.7
1973	6,250.3	959.3	3.6	1,887.2	902.7	21.8	88.8	10,113.7	15,818.1
1974	3,076.6	1,493.6	10.6	1,811.6	1,238.5	0.9	215.8	7,847.6	11,198.1
1975	4,455.5	1,691.2	14.3	414.7	1,874.6	0.3	255.4	8,706.0	11,334.8
1976	4,326.3	2,237.3	18.1	524.3	1,215.1	0.7	149.4	8,471.2	10,487.2
1977	4,563.1	5,228.8	365.0	428.6	880.3	0.2	353.2	11,819.2	13,804.7
1978[h]	490.4	3,740.0	1,351.0	312.0	1,167.3	0.1	330.7	7,391.4	8,041.8
1979[h]	2,184.5	2,525.0	4,208.0	97.5	1,309.5	1.5	226.0	10,552.0	10,552.0

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[a] Sources: California Department of Fish and Game, Fish Bulletins, California Marine Fish Landings, 1960-1976; Statistical Report of Fishery Products, 1977; unpublished preliminary estimates, 1978-1979; U.S. Dept. of Commerce, Fishery Statistics of the U.S., 1960-1975; Fisheries of the U.S., 1975-1979.

[b] Anchovy reduction landings, southern permit area.

[c] Total landings, all vessels.

[d] Total landings, all vessels, in California waters, 1960-1977; estimates for 1978-79.

[e] Landings by a group of vessels described by CF&G as wetfish, So. Calif. pelagic, or small (class 1 or 2) purse seiners, 1960-1976, estimates for 1977-1979.

[f] Total landings, all vessels.

[g] Landings by purse seine and lampara vessels, 1960-1975; estimates for 1977-1979 (excludes landings by dip and brail gear).

[h] Preliminary estimates, CF&G.

[i] Values adjusted for inflation by GNP implicit price deflator, 1979 = 100.

simple model of fishing costs representing a typical 58-ft purse seiner. Combs [1977] provides an estimate of minimum operating cost per ton landed of $24.58. Given that the better vessels averaged 78.1 ton/day fished in 1975, the daily operating cost is estimated to be about $1920. A vessel with this daily cost had a new price of about $425,000 in 1978.

The relationship between daily catch rate (i.e., catch per effort) and anchovy stock size has not been established, but MacCall [1976] has examined the relationship for sardines.[11] Since the sardine fleet operated in a fashion similar to that of the anchovy fleet, we may borrow the shape of the catch curve from the sardine fishery and then rescale it to the 1975 anchovy catch per effort. MacCall's equation introduces a nonlinear catch curve by specifying that the "catchability coefficient" be a function of fish stock biomass, B, so the catch equation becomes:

$$y = qfB \tag{6}$$

with $q = aB^b$

Inserting the estimated value of b (= −0.6) into Equation 6 gives us

$$y = afB^{0.4} \tag{7}$$

Catch per effort, y/f, of 78.1 tons in 1975 corresponds to a biomass of 3.6 million tons. Placing these values in Equation 6 allows us to solve for a = 0.186. Furthermore, noting that operating cost per day for a standard vessel is fixed at $1920, we can specify the operating cost per ton as the following function of stock biomass

$$C_1 = 10315\ B^{-0.4} \tag{8}$$

This operating cost function and the capital cost of $425,000 per vessel represents the known cost structure of the reduction fishing fleet.

Fish reduction plants in Los Angeles, Port Hueneme and Monterey produce fish meal, fish solubles and fish oil from anchovies. The product yields per ton of fresh fish processed varies among fish species, and, for a given species, among seasons of the year. The average product yields per ton of anchovy landed are:

Meal:	0.182 ton (348 lb)
Solubles:	0.112 ton (224 lb)
Oil:	0.0384 ton (76.8 lb)

Oil yield is especially variable, ranging from 140 lb/ton in September to 38 lb/ton of anchovy in the spawning season, February-April.

The meal and liquid solubles are sold as protein supplements for use in feeds for chickens, turkeys and freshwater fish. Local southern California poultry farmers buy most of the local fish meal and solubles. Imported anchovy, tuna/mackerel mix and menhaden meal from the Gulf and South Atlantic coasts are nearly perfect substitutes. Also, meat and bone meal from beef is a close substitute, and various vegetable protein meals (especially soybean and cottonseed meal) are readily available alternative sources of high-protein meal for poultry rations. Due to the cost-minimizing behavior of poultry growers and the ease of substitution, anchovy meal demand is naturally highly elastic. The only sources of market advantage for southern California anchovy meal seem to be (1) its higher protein content as compared with local tuna/mackerel and soybean meals, and (2) the cost of transporting fish meal to California from more distant production sites. A single-equation, linear least squares estimate of the inverse demand curve contained in Department of Commerce [1978] and Huppert et al. [1980a] is

$$p_m = 359.13 - 1.147\, q_m \tag{9}$$

where p_m is price per ton of meal and q_m is annual quantity of meal produced (in thousands of tons).

Neither the fish solubles nor oil markets for anchovy have been investigated sufficiently to yield similar, quantitative estimates of demand curves. Instead, we adopt a fixed-price for oil and solubles based on the average prices observed during 1970-1977. The average price of 12.87 ¢/lb for anchovy meal, implies a contribution of \$9.88/ton of anchovies processed. Similarly, the average price for solubles was \$105/ton, which converts to \$11.76/ton of anchovies. Assuming these fixed prices, and converting the anchovy meal price equation to a function of fish landings (landings equal 5.5 times meal produced) we get a "value per ton landed" equation

$$v = 86.9 - 3.795 \times 10^{-5}\, y \tag{10}$$

where y is annual landings. Although a more comprehensive study of the market demand would undoubtedly yield a more precise valuation procedure, Equation 10 provides a useful, rough estimate of the market value of reduction fishery harvests.

The industry structure in southern California is characterized by buyer and seller concentration in the raw fish sector, and by rigorous competition in the product markets. That is, the fishing fleet is organized by two unions—Fishermen's and Allied Workers Union (ILWU) and Fishermen's Union of America

(AFL-CIO)–and a vessel owners cooperative–the Fishermen's Cooperative Association of San Pedro. Fishermen in Monterey (or Moss Landing) are also represented by a chapter of the Fishermen's Union of America, but the few vessels landing at Port Hueneme apparently operate without benefit of a special organization. Buyers of anchovies for reduction are distributed as follows: one in Moss Landing, one in Port Hueneme and two in Los Angeles harbor. Competition in the fish meal and oil markets is assumed due to the large numbers of buyers and the plethora of alternative sources of both fish meal and other protein meals.

Because of the close-knit structure of the fishery/processor sector in all the reduction fishing ports, prices and wages are not a competitive market solution. Instead, the net value of the intermediate products sold is distributed to the various participants (reduction plant operators, fishing vessel owners, and crew members) through negotiated pricing and crewshare agreements. As is typical in marine fisheries, the crew members are paid a share of the landed value of the catch less direct operating expenses. Current arrangements call for a 58% share of the net landed value to be split among the 12-man crew.[12] The crewshare is negotiated between the Fishermen's Cooperative and the unions. Similarly, the Fishermen's Cooperative (with active guidance by the unions) negotiates a pricing formula for anchovy landings. The 1978 formula was

$$p_f = \begin{cases} 25 + (p_m/65 - 3) \times 7.5 & \text{if } p_m/65 \geqslant 3 \\ 25. & \text{if } p_m/65 < 3 \end{cases} \tag{12}$$

where p_f is price per ton of fish and p_m is price of fish meal quoted in the Department of Agriculture's *Feed Market News* (Los Angeles, California). Thus a meal price of $390/ton results in a fish price of $47.50/ton. This pricing agreement is analogous to the contingent contracts commonly signed by labor unions (see, e.g., Hall and Lilien [1979]). In this regard it is noteworthy that the minimum price of $25 is just above the estimated minimum average cost of $24.58/ton harvested. This strongly suggests that the ex-vessel fish price is related to the opportunity costs of fishing.

Processing of anchovies is estimated to cost $23.30/ton of fresh fish landed (D. Cukierman, personal communication). This cost is, of course, dependent on the rate of flow through the reduction plant to some minor extent, but this fact will be ignored in subsequent discussions. Combining this constant processing cost, the fishing cost (Equation 8), and the gross market value (Equation 10), the net economic profit for the consolidated fishing/processing sector is expressed as

$$NV = (63.6 - 3.795 \times 10^{-5} y)y - (10315 B^{-0.4})y \tag{13}$$

where capital costs of plant and vessels are not yet introduced.

The economic parameters and functional relationships described here are used in the following section on applications of economic theory to anchovy management. Table III presents a summary of these. Clearly, however, the broader economic concerns of nonreduction fishing and the ecological function of anchovies are as important as the quantified reduction fishery. The economic description of the fishery focused on the reduction fishery because the harvest for reduction is the major use of anchovies commercially, and because the data and analyses needed to quantitatively consider the other uses for anchovy are not available. As management analysts, however, economists must avoid the tendency to emphasize the importance of those things that are quantified to the neglect of those that are not.

THEORY AND ANALYSIS OF ECONOMIC ISSUES

Each of the five issues discussed in the second section above can be examined from the viewpoint of economic theory. The two issues which are most extensively and satisfactorily treated are those regarding optimum (i.e., economically efficient) reductions harvest rates and optimum investment in fishing capacity. Because these two issues are closely linked in the theoretical model they are combined in the first part of this section. Following this, the discussion turns

Table III. Economic Parameters and Functions for the Anchovy Reduction Fishery

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1. Inverse demand equation for processed products:

$$v = 86.9 - 3.795 \times 10^{-5} q_f$$

where v is value per ton of fish landed and q_f is tons of fish landed.

2. Average variable cost per ton landed:

$$c_1 = 10315\ B^{-0.4}$$

where B is stock biomass

3. Capital cost of fishing fleet:

$$c_2 = 425{,}000\ N$$

where N is number of fishing vessels in the fleet.

4. Cost of processing per ton landed:

$$c_3 = 23.30\ q_f$$

to the allocation issue. Both the allocation of anchovies to the live-bait fleet and to the enrichment of the ecosystem are important aspects. A brief discussion of regulatory mechanisms for managing the fishery precedes the final section which presents an economic approach to determining the "best" level of precision to attempt in measuring the stock size. Where data and/or appropriate theory are lacking the deficiencies are noted.

Optimum Harvest Strategies and Fleet Size

The term optimum harvest *strategy* emphasizes the need for a contingency plan, that is, for a harvest plan which adapts to the unpredictable variations in fish stock size brought about by oceanographic and ecological events. A substantial portion of existing theory assumes a deterministic world in which biological and economic relationships are known and predictable. Even the more recent dynamic optimization theorists [Brown 1974; Clark 1976; Quirk and Smith 1970] examine the characteristics of the long-run steady-state in great detail, while treating very briefly the problem of approaching a steady-state, and ignoring entirely the need for adaptive control in a fluctuating environment. This is not to criticize the development of dynamic, capital-theoretic analysis of fisheries, because substantial gains in understanding have resulted from these developments. But recent papers by operations researchers and mathematicians have explored the theory and solution methods for stochastic optimizing models (cf. Walters [1975]; Walters and Hilborn [1976]; Reed [1979]; Mendelssohn [1980]). These focus on the derivation of optimum harvest strategies with uncertain biological production parameters. The consequences of market uncertainty, measurement error and social aversion to variability have yet to be adequately examined in the fisheries context.

The first step in applying an optimization method is, of course, the adoption of a management objective. Ignoring for the moment the nonreduction uses and ecological linkages important to anchovy management, we define an economically optimal harvest strategy as one which sets the harvest annually to maximize the expected discounted value of the fishery. In any year the net value of the fishery equals the net profit to the fishing industry plus any consumer's surplus obtained by those purchasing the fish meal, oil and solubles. Profit to the fishing industry was examined above, but the existence of surplus is less transparent because the usual notion of consumer's surplus applies only to markets for final consumption goods. Fortunately, Just and Hueth [1979] have shown that under certain conditions the overall welfare effect of a change in quantity of an intermediate good is represented by the usual "area under the demand curve" associated with consumer's surplus. The intermediate good must be in a vertical chain of markets none of which has a perfectly elastic demand curve.[13] An acceptable procedure, therefore, is to combine the area under the demand curve but above the current market price with the industry profits to obtain an overall economic value. Based on Equation 13 the resulting algebraic expression is:

$$NEV(y,B) = (63.6 - 1.8975 \times 10^{-5}y)y - (10315B^{-0.4}y) \qquad (14)$$

where we ignore capital costs for now.

The long-run objective, the net present value (NPV) of the anchovy fishery over a period of T years, is computed by the usual formula:

$$NPV(y,B) = \sum_{t=o}^{T} NEV(y_t,B_t)\,(1/1+d)^t \qquad (15)$$

where d is a discount rate and $(1/1+d)^t$ is the discount factor applied to a monetary return occurring t years in the future. To introduce the random variability exhibited by the anchovy stock, the stock transition equation is multiplied by a lognormal error term ϵ.

$$B_{t+1} = g(y_t,B_t)\epsilon \qquad (16)$$

where ϵ has a mean value equal to one.[14] The function g( ) is the mean or expected stock transition function. Assuming that the public decision-maker is not averse to risk per se, the objective can be reexpressed as the expected net present value,

$$EPV = E(\sum_{t=o}^{T} NEV(y_t, B_t)\,(1/1+d)^t) = \sum_{t=o}^{T} E\,(NEV(y_t, B_t)\,(1/1+d)^t) \qquad (17)$$

The problem of maximizing the EPV subject to a stochastic stock transition equation can be decomposed into a sequence of annual decisions, each of which requires that the EPV be maximized for all future years, given the current stock biomass, B_t. Thus in year 1 the problem is to maximize

$$EPV_1 = NEV(y_1, B_1) + E(\sum_{i=2}^{T} NEV(y_i, B_i)\,(1/1+d)^i) \qquad (18)$$

It is most practical to solve this sort of problem with stochastic dynamic programming methods. The reader is referred to Hillier and Lieberman [1967] for a thorough introduction to the mathematics, but a common sense interpretation of the process is attempted here.

Equation 18 indicates that there are two ways to utilize the available biomass in any year. One is to harvest the fish, thus enjoying an immediate economic return. The other is to leave the fish in the ocean to contribute to the stock available in future years, thus increasing the potential future economic value. The current value of harvesting fish is subject to diminishing returns. and is dependent also on the current fish stock biomass, since unit harvesting costs are lower with greater biomass. The diminishing marginal value of catch discourages any tendency to harvest all the fish at once, and the decrease in harvesting costs resulting from larger biomasses provides one incentive for maintaining a larger fish stock. In addition, the expected percentage rate of growth in the fish stock grows as the stock declines, thus increasing the incentive to "invest" in the stock rather than to "liquidate" it when the stock is small. These various incentives are countervailing to some extent. Larger biomass means lower harvesting costs, but also lower percentage returns to investment in the stock. Thus the optimum policy must choose a trade-off between current and future returns which properly accounts for the impact of current harvests on the future. At the optimum current year harvest, the marginal value of additional catch just equals the marginal decrement to expected discounted value from future years.

Since the current value of a given level of harvest is enhanced by increased biomass, and since the percentage rate of growth in the stock is negatively related to biomass, we should expect larger current year biomass levels to be associated with greater current year harvests in the optimal program. That is, the optimum harvest strategy (optimum harvest as a function of, or contingent upon biomass) has a positive slope. A second common sense result is that there may be a biomass level below which the marginal value of current harvest is less than the expected contribution of increased biomass to future return for *any* positive level of harvest. That is, below some minimum biomass the optimum decision is to harvest none at all.[15]

The optimal harvest strategy for the anchovy reduction fishery, assuming no fishing capacity constraint and no other users of the resource, is displayed as Strategy I in Figure 4. This optimal strategy was computed assuming a discount rate of 0.04,[16] and a standard deviation of 0.3 for the proportional random error term in the stock transition equation.[17] To facilitate an interpretation of this harvest strategy, the expected yield curve from Figure 2 is reproduced on Figure 4. According to this optimum strategy, when biomass is below 1.1 million tons, the potential future return from investment in the stock exceeds the current net economic value of even a small harvest. At biomass levels between 1.1 million and 2.6 million tons, the optimum harvest is less than the expected growth in the stock, thus reflecting investment in a larger stock. Above a biomass of 2.6 million tons the optimum strategy calls for a drawing down of the stock, or dis-investment in biomass.

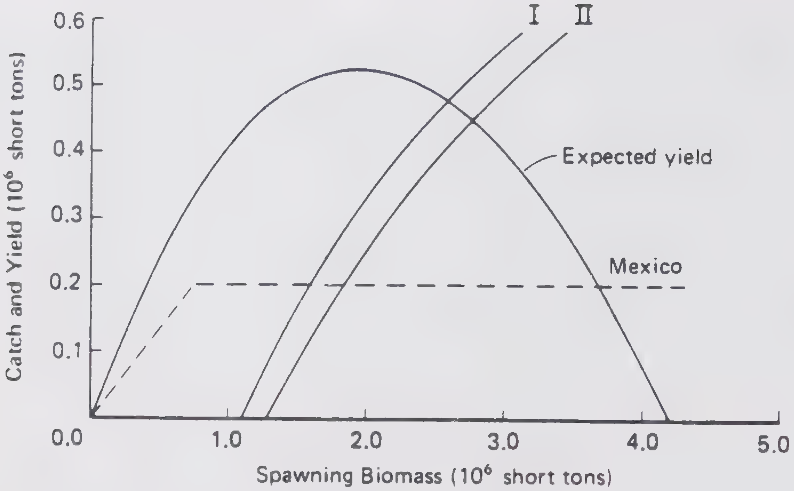

Figure 4. Optimal harvest strategies for the U.S. reduction fishery. Curve I is for fishery without Mexican competition. Curve II assumes Mexico takes an amount represented by the broken line.

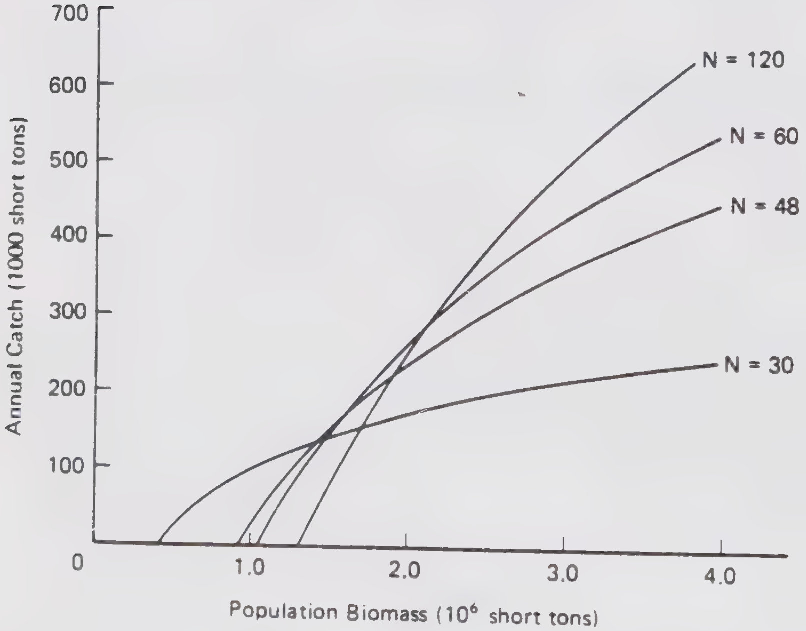

Figure 5. Optimum harvest strategies for the U.S. reduction fishery with fleet size constraints ranging from 30 vessels to 120 vessels. (Still assume Mexican harvest is as depicted in Figure 4.)

As explained earlier, the Mexican fishery for anchovy reduction at Ensenada expanded to an annual harvest of around 200,000 tons, most of which is from the central subpopulation of anchovies. If we assume that Mexico will continue to take 200,000 tons per year, the optimum U.S. harvest strategy is altered. Since reduced stock size would affect the Mexican fishery, we assume that no more than 90% would be taken of the 30% of the stock below the U.S./Mexican border. Given this admittedly arbitrary assumption, the U.S. strategy calls for a lower U.S. catch at every stock size (approximately 50,000 ton/yr lower than without the Mexican fishery), and an increase in the fishery cut off level of biomass from 1.1 to 1.3 million tons. Additional consideration of international strategies for harvesting the jointly fished stock along lines outlined by Anderson [1975] may be useful, but this requires economic data regarding the Mexican fishery that are unavailable to the author.

In deriving harvest strategies I and II in Figure 4, only the operating costs for fishing vessels and reduction plants were subtracted from the gross value in computing NEV. This is equivalent to assuming that fishing effort is unlimited. But the capacity for catching anchovies is limited by both the number of vessels and the stock abundance. Assuming each vessel fishes 144 days per year, the amount of nominal fishing effort available per year is $N \times 144 = f_{max}$, where N represents number of homogeneous anchovy fishing vessels. Inserting this and the estimate value for the parameter "a" into Equation 7 yields the following capacity constraint:

$$y_{max} = 26.78\ N\ B^{0.4} \tag{19}$$

The existence of such a constraint will alter the optimum strategy if some of the potential harvest rates along the unconstrained strategy curve (Strategy curve I in Figure 4) require more than the available fishing effort. With a fishing fleet of 48 vessels, for example, harvest strategy I exceeds the capacity output when biomass exceeds 2.57 million tons.

Optimum U.S. harvest strategies for a range of fleet sizes (and, again, assuming that Mexico harvests 200,000 tons) are displayed in Figure 5. As shown, diminishing fleet size dictates a falling harvest cutoff level and a lower peak catch level. For any one of these strategy curves the variations in biomass due to natural, unpredictable events will cause the fishery to harvest different amounts in different years. A frequency distribution of annual catches will be generated for any strategy and underlying error distribution in the biomass transition equation. Since the capacity constraint limits annual catch, it truncates the frequency distribution of catches on the righthand tail. A larger capacity, therefore, permits the fishery to take the larger catch consistent with large biomasses. But since the optimum strategy, with no capacity constraint, has an equilibrium harvest of around 470,000 tons (at an equilibrium biomass of 2.6 million tons), a capacity to take, say, one million tons might not be economical. A huge capacity would be used very infrequently; hence, the marginal expected value of an additional vessel must become very small for fishing fleets very much larger than that needed to take 470,000 tons.

One could define the optimum fleet size as that number of vessels which maximizes the net discounted value of the fishery minus the capital cost of building the fishing fleet. The curve labeled NPV in Figure 6 is the maximum net present value of the U.S. anchovy reduction fishery as related to fleet size. Each point represents NPV over a 25-year period. Only operating costs are considered in NPV, so the investment needed to build a fleet of N vessels is represented separately by the line labeled "capital cost." This line assumes each new vessel costs $425,000. It is easy to see that the maximum net difference between NPV and fleet capital cost occurs at a fleet size of about 48 vessels.

Assuming the absence of any recreational, ecological or income distributional concerns in the anchovy fishery, the economically efficient U.S. harvest strategy is the one labelled "N = 48" in Figure 5, and the optimum fleet size is 48. While this result is by no means conclusive (note the many qualifications in the previous statement), it provides a useful quantitative assessment of how economic considerations cause optimum yield to deviate from maximum sustained yield. Despite further modifications to incorporate noncommercial and noneconomic considerations into the optimum harvest strategy, two points will continue to be essential. First, the optimum harvest strategy is a contingency plan (or feedback control) which adapts current harvests to current stock levels for longer-term objectives. And, second, the optimum fleet size must be determined in a stochastic context which recognizes that all vessels will be fully utilized only infrequently.

Some of the key deficiences in the foregoing economic analysis are (1) the lack of multifishery interactions considered in the single-species optimizing framework; (2) the lack of market uncertainty in the model; and (3) the crudeness of estimated economic parameters such as those in the unit harvesting cost function, the demand function and the capacity relationship. Fishery interactions are particularly important for the southern California purse seine fleet as illustrated by the catch data in Table II. Since the capacity to fish is not specific to anchovy fishing, neither is the capital cost of the fleet. Furthermore, the opportunity costs of not fishing for, say, bonito or mackerel may frequently be greater than the current net return from anchovy fishing for many vessels. Thus the optimum rate of anchovy harvest ultimately depends on many other biological and market conditions. Before better multifishery models can be implemented, however, I think that additional serious theoretical development must ensue, possibly along lines suggested by Huppert [1979] or Anderson [1980]. More precise data on the fishing fleet economic parameters are needed, since the optimality of the given policies depends so critically on these values and the existing information is partly dependent upon extrapolations and secondary sources.

Allocation Among End-Uses

In a sense the allocation of fish among uses should be a part of the optimum harvest strategy. Any harvest by the reduction fishery clearly preempts some other use of the fish, and this is properly done only after comparison of the reduction fishery value to the opportunity costs associated with other uses. A

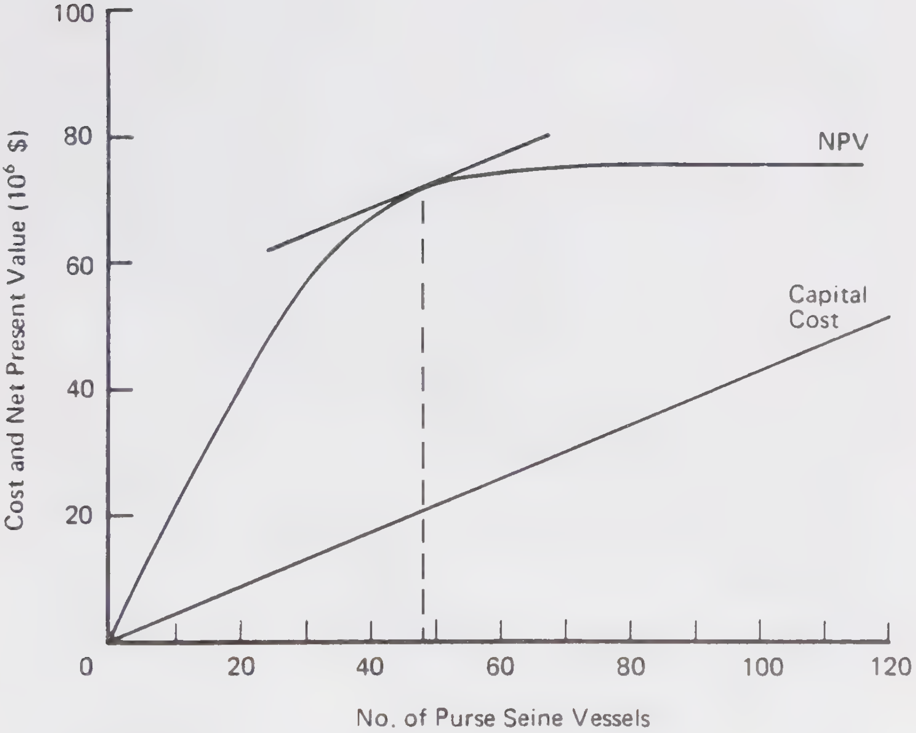

Figure 6. Net present value of the U.S. reduction fishery versus capital cost of the fleet.

more complete derivation of optimum harvests, therefore, would involve a more complicated economic value equation containing separate components for each end-use, and an additional constraint requiring the sum of the harvests to equal the total withdrawal from the population. An optimum harvest strategy with two end uses, for instance, would maximize the sum of two value expressions, NEV_1 and NEV_2. In most circumstances one would expect the optimum strategy to occur with an allocation of catch between the two uses such that the marginal values of fish in the two uses are equal.[18] In considering the allocation of anchovy harvest between reduction and live bait, however, no such analysis was performed.

To implement the theoretical model several additional pieces of information would be needed: (1) a demand curve for live-bait; (2) the costs of fishing for live-bait and holding the fish live; and (3) the physical relationship between reduction and live-bait fishing in the ocean. Available information suggests that such a formal analysis may be unnecessary. First, with respect to the third point, much of the live-bait fishing takes place nearshore during the late spring, summer and early fall. The "availability" of anchovy schools in the narrowly circumscribed baiting areas seems to determine the success of the live-bait operators in meeting contractual commitments to partyboats and in supplying the general public. The little evidence available does not suggest that the success of live-bait fishing is related to the anchovy stock size. If bait supply does not depend directly on the biomass and indirectly on the reduction fishery harvests, the need for treating the two fisheries as two competing users in an analysis of optimum harvesting strategy is negated. Furthermore, the small size of the live-bait harvests means that there is no detectable impact directly on the fish stock and indirectly on the reduction fishery. Given this perception of the situation, the arbitrary assignment of a portion of the overall harvest quota to the live-bait fishery (which is essentially the procedure followed in the Anchovy Fishery Management Plan) may be a perfectly acceptable resolution to the problem.

The other form of allocation, between harvest of anchovies and forage for higher-level predators, is not so easily dispensed with, but is even less amenable to analysis with existing empirical knowledge. Again, the theoretical format for determining an optimal harvesting program would have to be extended to include other sources of economic value. Since anchovies are preyed on by many commercial and recreational fish, the number of values would be great. The problem is further compounded by the fact that the recreational values are difficult to measure and the ecological models available are only suggestive of the structure of the interspecies relationships, not useful, predictive tools of analysis. In a general, qualitative sense, however, an optimum harvest strategy recognizing the ecological-cum-commercial and recreational value of anchovies as forage would harvest the stock more conservatively than the strategies without such recognition.

Choice of Regulatory Tools

There are several good surveys of fishery regulations. Crutchfield [1961; 1979], Anderson [1977], and Clark [1980] are particularly complete. The usual array of management methods includes annual fishery quotas, individual fisherman quotas, limitations on the kinds of gear used, limitation of the numbers of fishermen or vessels licensed, restriction of the fishery to certain areas or seasons, taxes or royalties on fish landings, and license fees. A few generalizations can be gleaned from the literature. First, in the face of severe fish stock depletion under open competition, any aggregate limitation on total annual withdrawals from the fish stock is beneficial if it enables the fishery to sustain a much higher harvest level. More consumer's surplus is generated even if no further efforts are directed toward productive efficiency (cost minimization). Second, a complex set of physical restrictions on fishing activities (such as gear, season, area and size limit regulations) may maximize the physical yield of the fishery, but so long as other dimensions of fishing effort are open to manipulation (at a cost) a competitive fishing industry will be unlikely to achieve a high degree of economic efficiency. To approach the socially optimal configuration of productive factors in the fishery as well as the ideal harvest rate requires either (1) an infinite degree of control over the individual fishing operations, or (2) a set of rules and conditions which elicits fishermen behavior consistent with economic efficiency. A variety of taxing schemes and altered property rights regimes have been proposed in order to meet this second condition.

In the Anchovy Plan a great variety of regulations were proposed. These included (1) the establishment of a harvest strategy curve for the California fishery, (2) a size limit of five inches on the reduction fishery, (3) closure of nearshore areas to reduction fishing, (4) closure of the reduction fishery during the peak summer recreational fishing season and during the peak anchovy spawning season (February/March), (5) allocation of the quota to nonreduction fishermen and among reduction fisheries north and south of Pt. Buchon, (6) adjustment of the annual quota in response to imbalances in the ratio of male and female fish in the harvest, and (7) license limitation in the reduction fishery. Of these, only the last two were rejected by the Pacific Fishery Management Council. Economic analysis gave some support to the harvest strategy curve, but the fact that the curve finally adopted was nearly identical to the existing California state plan leaves open the possibility that inertia was the dominant factor. And the license limitation proposal which was motivated explicitly by the economic efficiency rationale found little support, ostensibly due to the absence of a hugely overcapitalized fleet The slight support given the license limitation scheme came, ironically, from both the commercial and recreational groups. The commercial interests were presumably intrigued by the possibility of forming a closed shop, and the recreationists were willing to opt for any regulation limiting the size of the commercial fishery. Economic efficiency considerations, in other words, held little sway in the decision-making process.

The analysis of alternative kinds of economic regulations in the anchovy fishery suffers from fundamental defects stemming from inadequacies in the existing theory. Even the primary motivation for regulating the fishery could be given further attention. The usual argument is that a freely competitive fishery will overfish the stock, if not biologically then at least economically. But, as Scott [1955] pointed out, a sole owner would operate the fishery efficiently. And more recently Clark and Munro [1979] have suggested that a monopsonist fish processor may also run an economically efficient fishery. In the anchovy fishery we have neither a sole owner nor a true monopsonist fish buyer, but the number of participants in harvesting and processing is small enough to make one wonder whether the negotiating game among the few might not achieve a reasonable degree of commercial efficiency even without public regulations. Thus a satisfactory model of the industrial structure and behavior of the reduction fishery might have serious implications for management.

The biggest remaining difficulty, of course, is that a commercial fishery will be efficient only producing what it can sell. Recreation and enhancement of other fish stocks might require protection by a government agency even if overcapitalization and depletion in the usual sense is not threatened. Under the postulated condition of efficient execution of commercial fishing, but with too great an annual take, a quota system may very well be found to be an efficient management device. This line of reasoning bolsters my long-held belief that almost any kind of regulation can be efficient in some situation, and that the real need is for much more comprehensive empirical work which specifies the true situation and feasible set of alternatives.

Another of the basic weaknesses in the existing literature on fisheries regulation is that it is mostly based on a static model of the fishery (except for Clark [1980]), and always assumes a deterministic world. The unrealistic conditions assumed in the theory can lead to distortions in the conclusions regarding optimal regulatory policy. Weitzman [1978] shows that if the cost of deviating from a regulatory target (like not achieving the ideal harvest or fleet size) is a quadratic loss function, then the optimal selection of quantitative standards (like a quota) and pricing-type regulations (like royalities and license fees) generally includes a mix of both types. Presumably the regulatory analyst has some model of firm behavior which allows him to forecast the response of firms to new rules. To the extent that the behavioral model errs in predicting behavior, pricing-type regulations will result in missing the target. Quantitative rules may more reliably achieve targets in some circumstances. Whether reliance on quantity regulations is preferable to pricing depends on the cost of missing the target as well as the accuracy with which behavior can be predicted. If, for instance, a slight deviation is very costly (the weight attached to the squared term in the quadratic loss function is large), and firm behavior is predicted with large errors, quantitiative restrictions on firms are preferable to price incentives. On the other hand, if the value of the regulated industry is fairly linear about the target and the regulator's model of the industry behavior is accurate, optimum regulations may rely heavily on price incentives.

Although this quick sketch does not reveal the full implications of Weitzman's work, and the results are not directly applicable to fisheries anyway, it does suggest some new directions for investigation. In particular, the seemingly vast gulf between adherents of the traditional quota/season-type regulations and the proponents of taxes and royalities may be partly bridged by a theory embedded in a world of uncertainty and stochastic decision-making. Both kinds of regulation may be optimal under some conditions, and a mix of regulations is probably called for in most situations. The ideal mix of regulations for the anchovy fishery have almost certainly not been found. To make much progress we need further conceptual thinking and data gathering. Until more is known about the system being managed and better management alternatives are devised, a rigorous case for different regulations in the anchovy fishery will not be developed.

Analysis of Management Information

Collection and analysis of management information is a continuing need under any kind of management program. It is needed to support law enforcement activities and regular changes in regulations and to enable the managing agencies to periodically assess the performance of the regulations and initiate significant reforms. Because the FCMA provides broad definitions and regulatory options, there is now increased pressure on fisheries managers to husband great masses of economic, social and ecological data along with the more traditional stock assessments. All this is, of course, essential if enlightened fishery policy is to address the wide range of issues required by law. But enlightenment is costly, and at some point the marginal cost of more information must exceed its marginal value. To determine the optimum amount of information-gathering in all the various fields of inquiry is a prodigious task. But some routine data-gathering activities having a clear purpose and a calculable impact can be evaluated with the help of decision theory and the economic theory of information.

Generally speaking, any decision-maker must continually choose among a variety of options based on more or less imperfect information. An important component of the uncertainty inherent in decision-making is uncertainty about objective facts, i.e., uncertainty about the "state of the world." Assuming that different decisions are optimal under different states, better decisions will be made when more precise information about pertinent aspects of the world is available. Decision theory provides a rational framework for using imperfect information, and, consequently, suggests a way to place an economic value on specific kinds of information.

To give an example from anchovy management, consider the annual quota decision which, according to the anchovy plan [Department of Commerce 1978], follows the rule

$$Q = \begin{cases} 0.333(B - 1{,}000{,}000) & \text{if } (B - 1{,}000{,}000) > 0 \\ 0. & \text{if } (B - 1{,}000{,}000) \leq 0. \end{cases}$$

where Q is the annual quota and B is the estimated biomass. Since B is a statistical estimate based on ichthyoplankton surveys, it is at best correct on average. When biomass is over- or underestimated the assigned quota deviates from the level intended, and the expected economic value of the fishery presumably suffers. To evaluate the amount of information collection which is warranted on economic grounds, we need to demonstrate two relationships: (1) the relationship between the expected monetary value (EMV) of the fishery and the quantity of data collected; and (2) the correspondence between cost of data and quantity of data.

A rough, but illustrative, application of this approach can be developed by assuming that some elementary sampling theory applies to anchovy biomass estimation. First, we assume that the standard deviation of the biomass estimate about the true value is inversely related to the square root of the sample size. As the sample size gets larger the standard error of the estimate shrinks. This corresponds to collecting more data to get more precision. Table IV, columns 1 and 2 show the postulated relationship. Second, the cost of making the biomass estimate is assumed to be proportional to the sample size needed. (See Table IV, column 3.) Finally, the expected monetary value of the fishery is calculated as the annual average NEV defined as in Equation 14 above. The procedure for calculating these expected values involves a simulation program which is explained in detail by Huppert et al. [1980b]. As we should expect, the EMV (Table IV, column 5) for the fishery fall with decreasing accuracy of the estimate.

The payoff associated with increased data collection (i.e., larger sample size) for this example can be evaluated by comparing increased EMV with increased cost at successive levels of precision. The pertinent computations are given in Table IV, column 5. When the sample size is increased from 125 to 163, for instance, the cost of sampling grows from $139,000 to $181,000, while the EMV increases from $3.787 to $3.838 million for a net increase of $39,000. As is indicated in the table, collecting more than 222 samples may not be justified by the economic gain.

A more careful and thorough analysis is needed before reaching a final conclusion here, because nonreduction fishery values were not incorporated, and because an increased year-to-year variability in the quotas accompanies the decreased precision in estimation. An aversion to instability in the fishery would shift more emphasis onto the precision factor. Evaluation of other types of management information may be approached with the techniques outlined above.

SUMMARY AND RECOMMENDATIONS

A rich variety of economic issues and analytical techniques has been discussed or mentioned in the foregoing sections of the chapter. Existing applications to the anchovy fishery were summarized, deficiencies were identified and directions for improvement were suggested. Insufficient data are

Table IV. Evaluation of Biomass Estimates for the Anchovy Reduction Fishery Management Program

Standard Error of the Estimate[a]	Sample Size[b]	Total Cost	Expected Monetary Value (EMV)	Increase in EMV minus Increase in Cost
			($1000)	
0.05	8000	8896	4155	−6647
0.10	2000	1113	4130	−1200
0.15	889	989	4095	−384
0.20	500	556[c]	4046	−141
0.25	320	356	3987	−71
0.30	222	247	3916	+12
0.35	163	181	3838	+39
0.40	125	139	3757	–

[a] Represents a proportional, not additive, error.

[b] Based on the assumption that 500 plankton samples yield a standard error of 0.2. Other values are computed by the use of the formula: $\sigma = \sqrt{s^2} / \sqrt{N}$

[c] This is the estimated cost for annual survey in Department of Commerce [1978].

perhaps the commonest kind of problem, but this mainly affects the precision of certain estimated parameters and not the structure of the economic analysis or the kinds of management options evaluated. The methodological weaknesses, however, stem from more fundamental defects in applied fisheries economics. Three areas in particular need of further development are (1) the valuation of indirect impacts of commercial fishing and unpriced outputs; (2) a theory of multiple-use fishing vessels which addresses the problem of optimizing a mix of harvests under conditions of biological and market uncertainty; and (3) an investigation of the industry structure with implications for management strategy.

Obvious components of the first area of investigation are the extension of ecosystem models to predict interspecies effects of anchovy harvests, and development of recreational fishery evaluations to determine the importance of changes in angler success rates. The specification of predictive ecosystem models may be a distant goal, but current efforts in the area of recreational economics give some reason for optimism. Unless the impact of the anchovy fishery on recreationists can be assessed, however, the recreational economics work may not contribute significantly to management practice.

It is clear enough that a single species fishery with a single-purpose fishing fleet is an unrealistic abstraction. I think it is equally clear that the unpredictability of catch rates and the variability of fish prices provide sufficient motivation for the observed level of flexibility designed into the multipurpose southern California purse seine fleet. To manage adequately the harvest of any one target species in this situation has unavoidable implications for the others. A useful line of research, therefore, is one which seeks to capture the essential features of the fleet's economic strategies and to approach the fishery management question within a multidimensional model.

Behavior of the fishing industry is all too often assumed to be perfectly competitive. Cooperative behavior (or competition among a few participants) yields different conclusions regarding the need for public intervention, especially if a reasonable degree of control can be exercised by the industry over total fishery withdrawals. Externalities and indirect effects not valued by the commercial fishery may still justify public participation in fishery management, but industry behavior may be anticipated to solve some of the requirements for economic efficiency. Thus, the kinds of regulatory mechanisms proposed might reasonably avoid addressing many internal industry efficiency problems. A thorough examination of industry structure and market behavior along traditional lines could, depending on the finding, lead to a significant simplification in the kinds of regulations economists need examine.

NOTES

[1] Participating in the analysis of the anchovy fishery were, in addition to the author, Dr. G. D. Stauffer, A. MacCall and J. McMillan.

[2] The causes were natural in the sense that direct fishery-induced mortality was not responsible. The rapid growth of the stock in the early 1960s may have been partly due to the sardine stock collapse which may be attributable to the sardine fishery.

[3] A coefficient of variation equals the standard deviation divided by the mean.

[4] Although the presence of larvae is clear evidence of adults, there is some indication that anchovy schools tend to move farther north in the summer and south in the winter. Since the major spawning activity occurs during February-April, the larva distribution may be farther south than the average adult fish distribution.

[5] Gulland's method for estimating potential yield requires an estimate of unfished biomass. Since the anchovy stock biomass ranged from 2.6 to 4.0 million tons during the 1968-1972 period, the potential yield was given as a range of 1.5 to 2.4 million tons (MacCall et al. [1976], p. 7). Clearly, the unfished stock of anchovies was far smaller in the early 1950s than it was in later years.

[6] Radovich and MacCall [1979] was first presented at the 1976 CalCOFI Conference. Thus it predates MacCall [1980] and Department of Commerce [1978].

[7] The statistical test is of the hypothesis $H_0: E(R/B) = \bar{R}$. The following table from Huppert et al. [1980b] summarizes the results for both recruitment models in Figure 3.

Analysis of Variance for Recruitment Models
(Total sum of squares equals 14.078)

	Model A (logistic)	Model B
Variance		
Explained (df)	4.506 (1)	3.875 (1)
Unexplained (df)	9.572 (13)	10.203 (13)
Mean Square		
Explained	4.506	3.875
Unexplained	0.736	0.785
F-statistic	6.12	4.94
Approximate probability	0.028	0.045

[8] The alternative recruitment model, B, was generated during a discussion of density-dependence at the Pacific Fishery Management Council's Scientific and Statistical Committee meeting in La Jolla, California on July 8, 1980. Below a biomass of 1.225 million tons the per capita recruitment is "density-independent" (i.e., not affected by the biomass of spawning fish), and above 1.225 million tons the absolute value of recruitment is density-independent. This model is a compromise between two extreme positions; one holding total recruitment to be completely independent, and the other holding recruitment to be strictly dependent via the logistic growth model.

[9] Green's estimated total predation was 3.5 times the estimated small school fish available to predators. The gap between these two figures illustrates the crude state of existing quantitative ecosystem models.

[10] The origin of the term "wetfish" is disputed among experts, but throughout this paper it stands for a group of fish species landed "wet" (i.e., in fresh seawater, without freezing) by purse seine vessels. These species include anchovy, jack mackerel, Pacific mackerel, Pacific bonito, bluefin tuna, Pacific sardine and squid. The "wetfish fleet" is that group of purse seiners which land these species *and* are smaller and less mobile than the tropical tuna vessels.

[11] An earlier unpublished paper by Fox [1974] precedes MacCall's work and the summary discussion by Gulland [1977] of the variable catchability model.

[12] The $24.58/ton average cost of fishing anchovies which was quoted earlier would correspond to an approximate $18,900/year wage per crew member. This assumes 48 weeks of fishing five days per week at 78.1 tons catch per day, direct operating costs of 15% of cost and 58% crew share for a 12-man crew.

[13] Strictly speaking, the Just and Hueth result applies only to a vertically structured competitive sector of an economy where each industry in the sector produces a single product using one major variable input produced within the sector and other variable inputs originating in other sectors of the economy. Since both the fishing fleet and the processing firms produce nonanchovy products, this use of their welfare measurement is not completely legitimate.

[14] Equation 15 can be derived from the stock transition Equation 4 and the catch Equation 5. Although we cannot algebraically solve Equation 5 for fishing mortality, F, as a function of y_t and B_t, there is a one-to-one correspondence between F and y_t and B_t which can be computed numerically and can be expressed as

$$F = f(y_t, B_t),\ y, B > 0$$

with $$\frac{\partial f}{\partial y} > 0, \frac{\partial^2 f}{\partial y^2} > 0, \frac{\partial f}{\partial B} < 0, \frac{\partial^2 f}{\partial B^2} = 0$$

Substituting this function into Equation 4 yields

$$B_{t+1} = B_t K/(H + B_t) - B_t e^{-(M-G)} (1 - e^{-f(y_t, B_t)})$$

or $$B_{t+1} = g(y_t, B_t).$$

[15] More formal derivation of these qualitative results proceeds as follows. The deterministic optimization problem is to maximize the following Lagrangian

$$L = \sum_{t=0}^{T} NEV(y_t, B_t) \left(\frac{1}{1+d}\right)^t - Z_t \left[B_{t+1} - g(y_t, B_t)\right]$$

Necessary conditions for an interior maximum are

$$\frac{\partial L}{\partial y_t} = \left(\frac{1}{1+d}\right)^t \frac{\partial NEV}{\partial y_t} + Z_t \frac{\partial g}{\partial y_t} \leq 0 \qquad (1)$$

$$\frac{\partial L}{\partial B_t} = \left(\frac{1}{1+d}\right)^t \frac{\partial NEV}{\partial B_t} - Z_{t-1} + Z_t \frac{\partial g}{\partial B_t} \leq 0 \qquad (2)$$

$$\frac{\partial L}{\partial Z_t} = B_{t-1} - g(y_t, B_t) = 0 \qquad (3)$$

$$y, B > 0$$

If $\frac{\partial L}{\partial y_t} < 0$ for all $y > 0$, the nonnegativity constraint is effective, i.e., the optimum y is $y = 0$. Note that Z_t is the discounted value of having one more unit of biomass in year $t + 1$. If B_t is not so low as to require a zero harvest, Condition 1 must be an equality. An interpretation of this is that the marginal contribution of catch in year t to the discounted return must just equal the marginal contribution of leaving an additional unit (i.e., catching one unit less). The second term on the right side of Equation 1 equals marginal contribution of an additional unit of stock next year times the marginal effect of this year's catch on next year's stock.

[16] Choice of an appropriate discount rate involves several theoretical nuances that are not of great concern here, but which have occupied the journal literature [Baumol 1968]. The 4% rate of discount reflects the typical yield on Moody's corporate AAA Bonds during the relatively non-inflationary 1950-1965 period.

[17] A sample standard error of about 0.6 was computed for the residuals of the growth model [Huppert et al. 1980b]. A smaller standard deviation is assumed here because much of the variability in the fitted residuals appears to be due to the less accurate biomass estimates of the early 1960s which were based on far fewer plankton samples than are current estimates. It seems reasonable that at least half of the original standard error could be attributed to variability in the stock's real growth response.

[18] Using the terminology of note 15 and substituting the relationships,

$$NEV(y_t, B_t) = V_1(y_{1t}, B_t) + V_2(y_{2t}, B_t)$$

$$y_{1t} = S_1 y_t$$

$$y_{2t} = (1 - S_1) y_t$$

into the Lagrangian expression, the necessary conditions for an optimum include the following:

$$\frac{\partial L}{\partial y_t} = \frac{\partial V_1}{\partial (S_{1t}\, y_t)}\, y_t - \frac{\partial V_1}{\partial (1 - S_{1t}) y_t}\, y_t < 0$$

In case this condition is satisfied as an equality, the marginal value of harvest in use 1 must equal the marginal value in use 2.

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A Corral System for Examining Pelagic Dolphin Schools

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ABSTRACT—A research platform was developed for study of schools of wild pelagic dolphins. The Porpoise School Impoundment System (PSIS) was designed to safely handle schools of up to 500 animals in a manner compatible with standard fishing procedures of tuna purse seine vessels. The PSIS attaches to the purse seine net to receive the dolphins as they are released from the net. The compartmentalized apparatus has a corral capable of holding up to 120 dolphins. The animals are maneuvered to chutes where they can be individually examined and prepared for other studies. They can be released individually or held in holding pens for release together. The PSIS was used during two cruises for coordinated studies involving capture of 1,319 dolphins. The system proved to be a safe and effective platform for open-ocean studies of wild dolphins.

Introduction

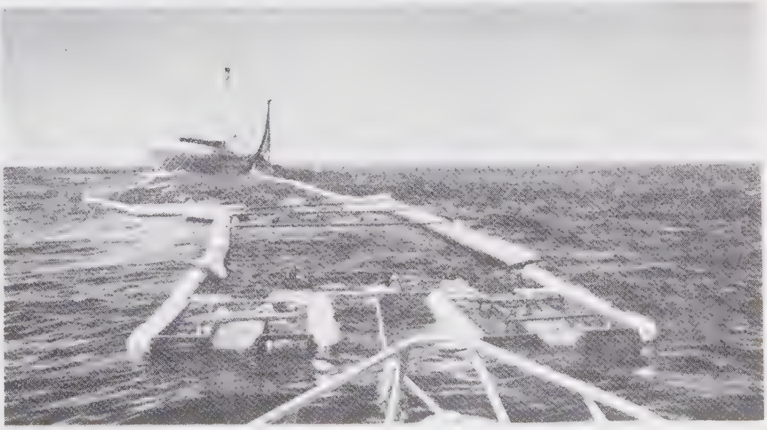
Several species of small cetaceans, primarily dolphins, are involved in the purse seine fishery for yellowfin tuna, *Thunnus albacares*, in the eastern tropical Pacific. Cetacean mortality in this fishery has been reduced from an average of 309,000 in 1971 and 1972 (Fox, 1978), to about 19,000 in 1978 (Smith[1]). This reduction in mortality is mandated by the Marine Mammal Protection Act of 1972, which also requires continual assessment of the dolphin stocks to assure that they are properly managed through regulation of the fishery.

Several assessment studies required a mechanism by which large groups of dolphins, caught by the tuna purse seiners, could be safely contained, examined, and released. These studies included examination of dolphin schools for species, age, and sex structure; investigation of school dynamics by radiotracking; and study of short-term school cohesion and integrity as well as long-term distribution and movements by tagging.

No system or technique existed for holding and handling whole dolphin schools; the species involved in the fishery have schools averaging about 500 animals. However, much information was available on the holding requirements of captive dolphins in pool enclosures. Standards for the handling and transportation of these animals have been developed by the U.S. Department of Agriculture (1979). Irvine (1970) described a lightweight, portable holding pen designed to be rapidly deployed at sea from a vessel or helicopter, but the pen was designed to hold only a single trained dolphin.

The primary design requirements were: 1) That the system be safe for dolphins and personnel alike while in the water and during deployment and retrieval from the vessel, 2) that the system be capable of holding whole dolphin schools of up to 500 animals for simultaneous release as well as for release of individual animals, and 3) that the system be compatible with the vessel's standard fishing operations.

During these operations, dolphins are released from the purse seine by a process known as "backing down," which involves the ship's manipulation of the



The Porpoise School Impoundment System in operation during a research cruise of the Cooperative Dedicated Vessel Program. Porpoise are being maneuvered from the tuna purse seine into the corral for examination and tagging.

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[1] Smith, T. D. (editor). 1979. Report of the status of porpoise stocks workshop (August 27-31, 1979, La Jolla, California). Admin. Rep. LJ-79-41, Southwest Fisheries Center, NMFS, NOAA, P.O. Box 271, La Jolla, CA 92038.

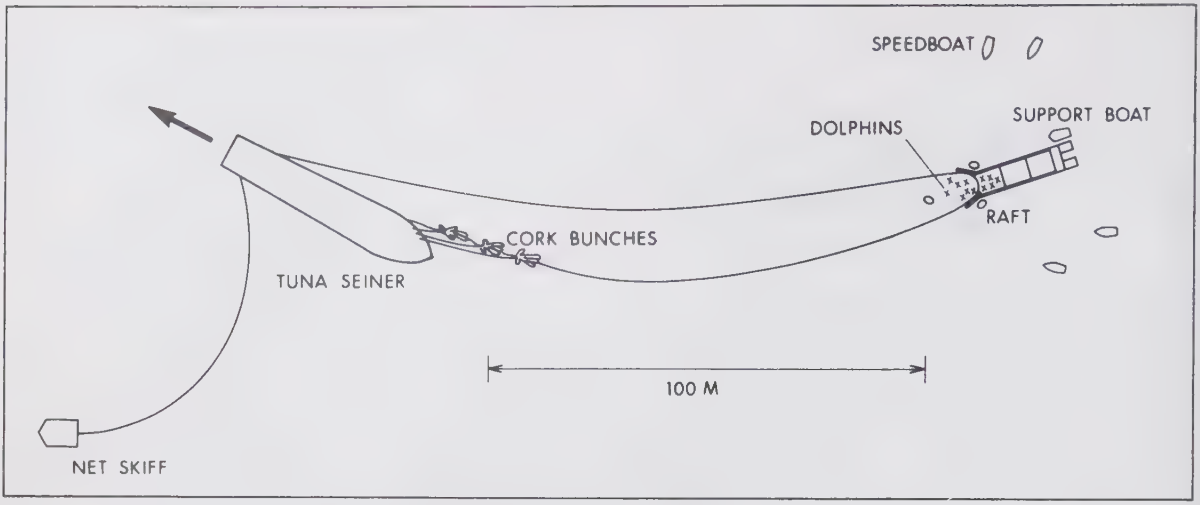

Figure 1.—The PSIS attached to the purse seine net during backdown.

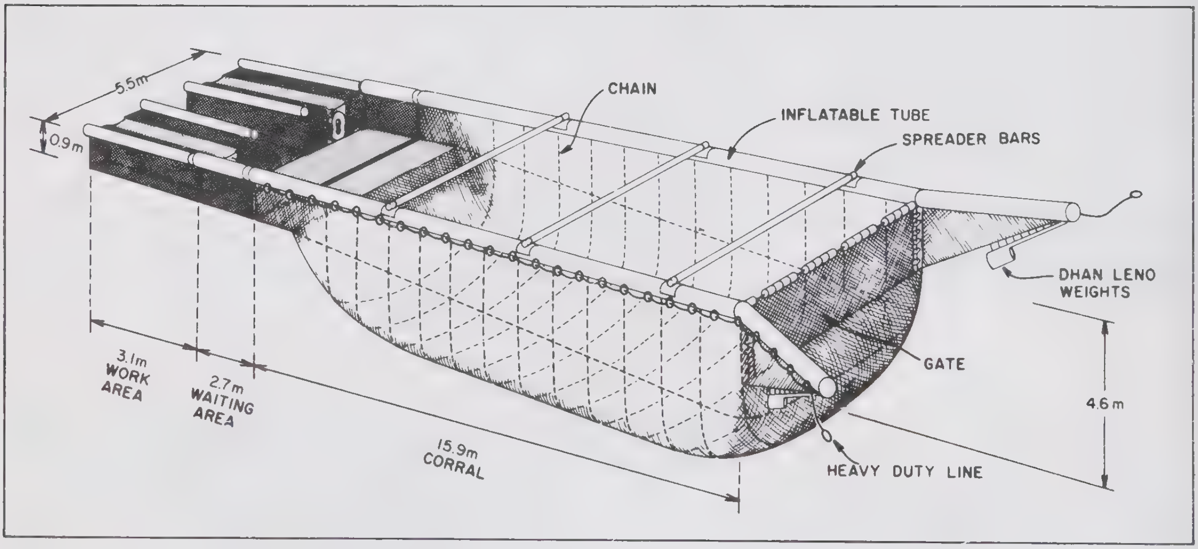

Figure 2.—The PSIS without the pens.

net into an oblong shape while the dolphins position themselves at the end farthest from the vessel. The net is then essentially pulled out from under the dolphins (Perrin, 1969; Coe and Sousa, 1972). The corral system was designed to be compatible with this release technique. It attaches to the backdown area of the net to catch the dolphins as they leave the purse seine (Fig. 1).

The research was made possible by the cooperation of the United States Tuna Foundation which provided the vessel, the *Queen Mary*, for a year to study the porpoise-tuna problem. The program was known as the Dedicated Vessel Program.

Materials and Methods

The Porpoise School Impoundment System (PSIS) (Fig. 2, 3) consists of a

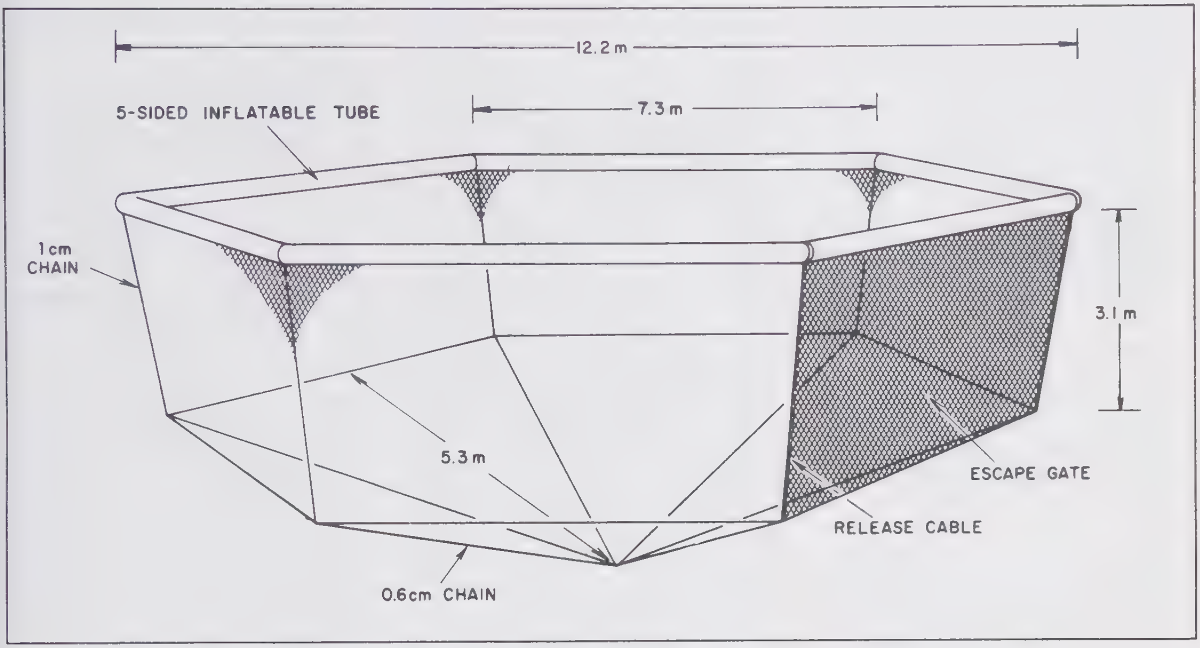

Figure 3.—A holding pen of the PSIS.

"corral" of webbing into which large portions of the school are transferred from the seine and held prior to examination; a "waiting area" of expanded aluminum mesh in which the dolphins are maneuvered individually to the chutes; two "work areas" with chutes in which the animals are measured, examined, tagged, etc.; and five "holding pens" in which groups of dolphins can be held until the school is released as a unit.

The dimensions of the corral and holding pens are based on estimated space requirements for temporarily holding individual wild dolphins. Minimum space is allowed in the corral, since the dolphins spend relatively little time in this component; allowing too much swimming room would complicate catching individual animals and prolong the operation. More space per individual is allowed in the holding pens where the dolphins could spend several hours. Both components allow for the estimated natural turning radius of 4.9 m required by an adult spotted dolphin (Pryor[2]).

The dimensions of the noncollapsible components were limited by the storage space available on the deck of the chartered medium-sized (500-ton) purse seiner and by the number of scientists the vessel could house to deploy, operate, and retrieve the PSIS. Modifications of the system were made after an initial feasibility cruise.

The Corral

The corral (Fig. 2) measures 15.9× 5.5 m, with the depth decreasing from 4.6 m at the mouth to 0.9 m at the waiting area. The shape at the surface is maintained by rigidly inflated 40.6 cm diameter nylon-reinforced polyvinyl tubes and 7.6 cm diameter aluminum spreader bars that mount into aluminum saddles on the inflatable tubes. The tubes are inserted through the sleeves formed of webbing. The weight of 0.6 cm and 1 cm galvanized chain is used to maintain the subsurface shape, especially when the corral is under tow during "backdown." Heavy-duty 2.5 cm braided nylon lines run along the base of the inflatable tubes to absorb the strain on the system when it is towed through the water. These lines run from steel rings on the purse-seine corkline to the work area. The corral weighs about 545 kg.

The corral attaches directly to the purse seine. The inflatable tubes are flared at 45° angles and have weighted net wings to prevent dolphins from escaping over the corkline and to funnel them through the gate of the corral. The gate consists of a 7.3×3.1 m panel of webbing with a corkline. The panel is lashed directly to the corkline of the purse seine, so that they sink and rise together during "backdown." After the dolphins are in the corral, the lashings are cut to allow the gate to rise, blocking the opening. When the last batch of animals is transferred into the corral, the PSIS is detached from the purse seine.

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[2] Pryor, K. 1979. Report to the National Marine Fisheries Service on sea tests of the Porpoise Impoundment System, March 3, 1979. Dolphin Behavior Consultant, 28 East 10th Street, New York, NY 10003.

A 4.6 m deep crowder net is placed in front of the gate and used to maneuver the dolphins toward the waiting area. The crowder net is hung from a floating polyurethane-foam bar and is weighted with chain. It is maneuvered with lines passed through pulleys in the waiting area.

The Waiting Area

The corral webbing attaches directly to a rectangular platform of expanded aluminum mesh buoyed by hollow, watertight support beams. Although the waiting area is neutrally buoyant, a series of 30 cm dock bumpers provides additional flotation in case any of the hollow members flood and protects the structure upon impact with the vessel during deployment and retrieval. The waiting area is about 5.5 m wide and 2.7 m long, with four walls, 0.9 m high. One wall is hinged to fold down when in use, extending the walking area by an additional 0.9 m. (When stored on the vessel, this wall is folded up to minimize space.) Standing waist deep in water, scientists can catch and lead the dolphins to the chutes. This component weighs about 454 kg.

The Work Areas

The two work areas are of construction similar to the waiting area. Each measures 3.1×1.8×0.9 m and contains a center chute with a walkway on each side. The chute of clear plastic is marked in 1 cm increments to allow for rapid measurements of dolphins. Polyurethane floats on both sides of the structure provide additional stability and safety. Interlocking automobile tires are placed between the waiting areas to allow for articulation between the components, to keep them aligned, and to prevent the aluminum structures from damaging each other. Each work area weighs about 182 kg.

The Holding Pens

Original research plans called for release of intact schools of up to 500 dolphins after examination and tagging. Five pens were designed to hold 100 dolphins each for up to 12 hours. In addition to allowing for more space per individual than allowed in the corral, the pens were designed without corners because wild pelagic dolphins do not negotiate corners. The pens are hexagonal and have sloping floors (Fig. 3). The hexagonal shape allows the pens to be efficiently clustered and monitored.

Each pen measures about 7.3 m on a side, 12.2 m in diameter, and has a center depth of 4.6 m. The subsurface shape is maintained by weighting the net with 0.6 cm and 1 cm galvanized chain. Nylon-reinforced polyvinyl inflatable tubes of 40.6 cm diameter maintain the hexagonal shape and keep the pen afloat. One side of the pen has a separate inflatable tube that is part of the release gate. The gate consists of a separate panel 7.3 ×3.1 m laced to the adjacent panels with plastic-coated steel cable strung through brass rings. When the dolphins are to be released, an aluminum spreader bar is placed across the opening, the inflatable tube is removed, and the gate is dropped by pulling the cables.

General Safety Features

All netting is of 3.2 cm stretch-mesh webbing, which has been demonstrated to minimize ensnarement of dolphin teeth and fins (Barham et al., 1977). In order to reduce abrasion of the dolphin skin, knotless webbing is used, all exposed metal edges have been filed smooth, and the expanded aluminum structures have been coated with a slick tar-based paint. All components of the system are attached so no gaps exist in which dolphins can get caught or through which sharks can enter. Heavy chains maintain the shape of the nets so that no "canopies" can form which might entrap the animals. Quick-release systems are designed into each component of the PSIS in case of emergency. The aluminum-mesh webbing provides protection from sharks. Extra flotation is provided in the event a hollow aluminum member floods, and battery-powered air pumps are available to compensate for any leaks in the inflatable tubes of the corral or holding pens. A complete above- and underwater lighting system has been developed in case operations continue into the night.

The PSIS was used during two 60-day research cruises aboard a chartered 500-ton fish carrying capacity tuna purse-seine vessel. The research was conducted in the vicinity of Clipperton Island off Mexico. The primary objective of the first cruise was to determine the feasibility of using the system to examine and tag whole schools of spotted dolphins, *Stenella attenuata*, of up to 500 animals. Capture and retention of whole schools was found to be very difficult, as portions of the school evaded capture or escaped when being transferred from the seine into the PSIS. Considerable caution was used while operational techniques were developed and environmental limitations defined. A total of 611 dolphins was captured in four net sets; 447 of these were examined for age and sex. The largest group consisted of 204 dolphins. A total of 17 dolphins was accidentally killed during the operation: 11 died in the seine or corral, 1 was killed by a shark outside the PSIS, and 5 died as a result of entanglement in the webbing. The cruise report[3] summarizes the results of the research.

Inadequate space on the vessel for storage of all five holding pens and for housing additional personnel prevented full use of the pens. One pen was used to hold 53 spotted dolphins for 7.5 hours, with no observable signs of stress and no mortality. Holding was terminated just after dark, otherwise no night work was done on either cruise.

During the second cruise, the PSIS served as a platform for a coordinated series of studies including examination for age and sex structure of schools, tagging for long-term movements, tetracycline injection for age determination, blood sampling for analysis of physiological capture stress, and radio-tracking for study of short-term school cohesion. During nine sets, 872 dolphins were examined, 656 were tagged with dorsal-fin tags, 331 received tetracycline injections, 49 had blood sampled, and 6 were radio-tracked for three 2-day tracking sequences. The largest group examined consisted of 164 spotted dolphins. Thirty-six dolphins were accidentally killed: 21 died within the PSIS, 14 died in the purse seine, and 1 died after being entrapped between the seine and the corral[4].

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[3] Coe, J. M., J. G. Jennings, C. B. Peters, and J. DeBeer. 1979. Research related to the tuna-porpoise problem: summary of research results from the second cruise of the Dedicated Vessel, 17 April to 5 June, 1978. Admin. Rep. LJ-79-6, Southwest Fisheries Center, NMFS, NOAA, P.O. Box 271, La Jolla, CA 92038.

Conclusions

The feasibility of using the PSIS as a research platform for study of wild pelagic dolphin has been demonstrated. One thousand three hundred nineteen (1,319) dolphins were successfully examined, with very low mortality. Although the system was never used to its design capacity of 500 animals, handling schools of this size should be possible if all conditions are ideal.

Major limitations on the use of the system include environmental conditions, species composition of the school, available daylight, and number of people available to operate the PSIS. To be safe, sea state should not exceed Beaufort 3 and winds should not exceed 12-14 knots. Special attention should be paid to impending weather. Spotted dolphins, *S. attenuata*, are generally calmer animals and are considerably easier to handle than are spinner dolphins, *S. longirostris*. The more active spinners require additional space and close monitoring because there is a greater risk of mortality or injury. Since it is advisable to conduct all activities in daylight, the time of day the school is found and operations can commence is critical. Generally, 5-6 hours are required from time of deployment to retrieval of the PSIS. Operation of the system without the holding pens requires 8-10 persons. A detailed operations manual[5] is being prepared.

The limits of the system are defined. The corral can hold a maximum of 120 dolphins, with no more than 50 spinner dolphins if the species composition of the school is mixed. While the largest school contained 204 animals, processing larger schools should be possible by repeatedly placing groups of about 120 dolphins in the corral during multiple backdowns. The maximum holding capacity for each pen is 75-100 dolphins.

Simultaneous release of animals from more than one pen would be difficult. The pens tend to collapse when being towed, and since the backdown procedure requires pulling the net through the water, a pen of dolphins would have to be set adrift with attendant personnel before backdown. The pens therefore could become widely separated. Additional personnel and boats would be required to monitor the pens and release all groups simultaneously. The dolphins would probably regroup after release.

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[4] Powers, J. E., R. W. Butler, J. G. Jennings, R. McLain, C. B. Peters, and J. DeBeer. 1979. Summary of research results from the fourth cruise of the Dedicated Vessel, 12 September to 31 October. Admin. Rep. LJ-79-14, Southwest Fisheries Center, NMFS, NOAA, P.O. Box 271, La Jolla, CA 92038.

[5] Coe, J. M., J. G. Jennings, R. W. Butler, and W. E. Stuntz. In press. An operations manual for the Porpoise School Impoundment System (PSIS). NOAA Tech. Memo., Southwest Fisheries Center, NMFS, NOAA, P.O. Box 271, La Jolla, CA 92038.

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RAPID COMMUNICATION

Induced Locomotion by Midbrain Stimulation in Restrained Skipjack Tuna, *Katsuwonus pelamis,* L.

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ABSTRACT We show that electrical stimulation of the midbrain of restrained and sedated skipjack tuna (*Katsuwonus pelamis*) produces coordinated locomotory activity. Therefore, our preparation is a viable alternative for creating normal swimming movements which can be closely controlled by the experimentalist, and demonstrates that a midbrain "locomotory center" is present in skipjack tuna, as in other teleosts. *Key words:* induced locomotion, midbrain stimulation, skipjack tuna, *Katsuwonus pelamis*

Because tunas are both highly active and physiologically very delicate, it is difficult to successfully force them to swim in a water tunnel. Most die immediately or survive for only a few hours under such conditions. Although the electromyograms (EMG) of swimming skipjack tuna (*Katsuwonus pelamis*) have been successfully recorded (Brill and Dizon, '79), only the simplest instrumentation can be employed on tuna to be swum in a water tunnel because the fish must be transferred from their holding tank to the swimming chamber quickly, or they will not regain equilibrium.

Normal locomotory movement can be induced by electrical stimulation of the brain (Kashin et al., '74) and spinal cord (Grillner, '74) of fishes. Such preparations allow better control of experimental conditions and thus greatly facilitate investigations of the parameters of locomotion. We therefore decided to investigate the feasibility of inducing coordinated locomotory movements in skipjack tuna by selectively stimulating regions of the brain shown to effect locomotion in other teleost species.

Our goals were (1) to locate the "locomotory center" in the brain of tuna, and (2) to produce a preparation where rhythmic swimming movements could be induced and controlled by electrical stimulation of the "locomotory center" in restrained tuna.

MATERIALS AND METHODS

We used four skipjack tuna, ranging in fork length from 39.4 to 40.0 cm and in weight from 849 to 915 gm. The fish were selected from stocks maintained at the Kewalo Basin Laboratory of the National Marine Fisheries Service (Honolulu, Hawaii). Nakamura ('72) provides details on the capture and handling of tuna at this facility.

Each fish was dip-netted, injected intramuscularly with 37.5 mg of anaesthetic (sodium thiopental), and returned to its holding tank.

When the fish could no longer swim (within 5 to 10 minutes), it was removed from its holding tank and placed in a plexiglass restraining trough. The head was clamped firmly to a stainless-steel seawater delivery tube that was placed in the fish's mouth for irrigation of the gills. The anterior half of the fish's body was held by foam rubber and plastic foam packed between the fish and the sides and the bottom of the restraining trough. The posterior portion of the fish, from the anterior margin of the anal fin to the caudal fin, was thus suspended in air.

The cranium roof above the cerebellum was removed. In some preparations, the forebrain was also removed in an attempt to prevent spontaneous locomotion. However, removal of the forebrain had no discernible effect on either the occasional bouts of spontaneous locomotory movements or on those induced by brain stimulation. Using a micromanipulator, monopolar or bipolar stainless-steel stimulating electrodes were pushed through the portion of the cerebellum that overlay the visual

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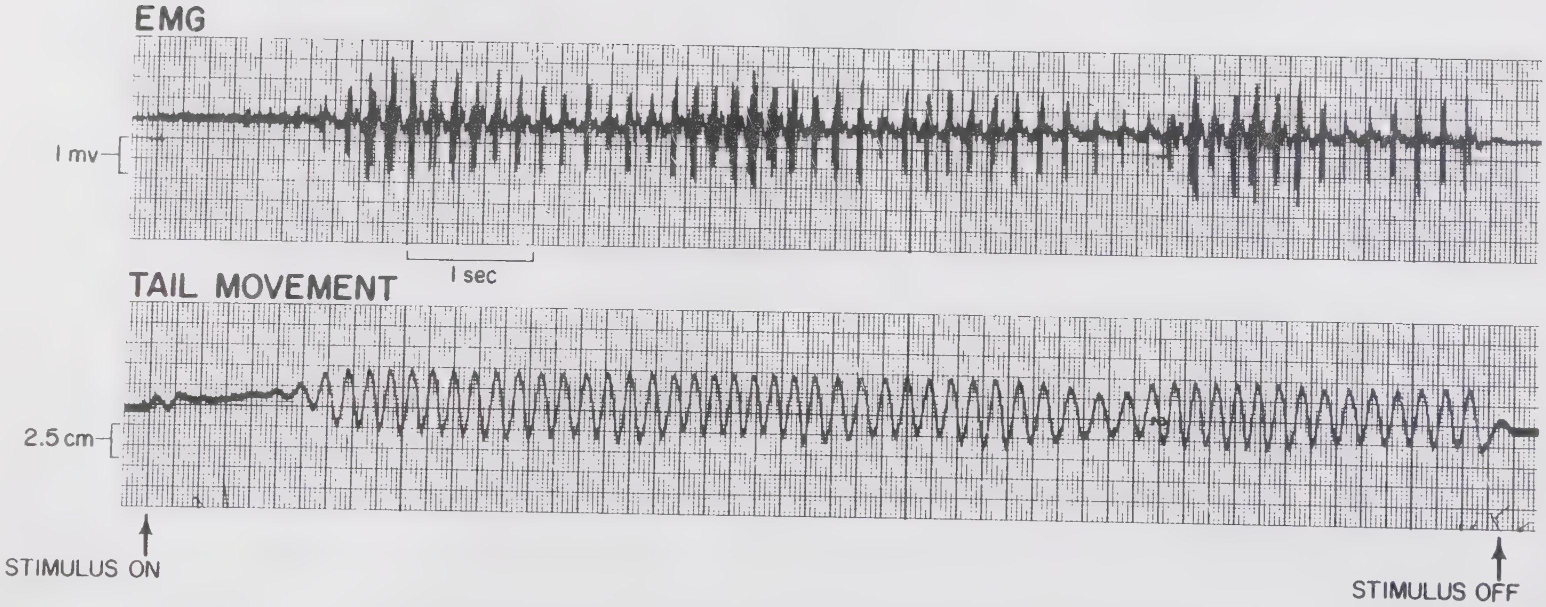

Fig. 1 EMG and tail movement recorded during brain stimulation. The EMG electrode was inserted into the red muscle portion of the myotomes on the right side of the fish; upward pen movement indicates tail flexure to the right.

lobes and into the midbrain. The electrodes were insulated needles with the uninsulated tips measuring 1–2 mm. The ends of the electrodes were positioned approximately 9 mm below the surface of the cerebellum. Both monopolar and bipolar square-wave stimulation were applied. The duration of the stimuli was 1.5–5 msec, the frequency 80–120 Hz, and the applied voltage 0.1–5 volts.

Muscle activity was monitored by EMG electrodes inserted into the lateral red muscle behind the dorsal fin. Tail movements were measured by a rotary potentiometer that was suspended directly above the caudal fin, and attached to the caudal peduncle by an aluminum rod. EMG and tail movements were recorded simultaneously on a two-channel pen recorder.

Additional intramuscular doses of sodium thiopental (25 or 37.5 mg) were administered occasionally to keep the fish quiet.

RESULTS

We found that skipjack tuna have an area in the midbrain, the so-called "locomotory center," which produces symmetrical rhythmic swimming motions when stimulated. The best point of stimulation is along the midline of the brain in the caudal part of the optic lobes, 9–11 mm under the surface of the cerebellum. (In tunas, the corpus cerebelli is elevated forward, covering the optic lobes.) Swimming movements started shortly after the stimulation began, continued as long as stimulation was applied, and ceased as soon as stimulation stopped (Fig 1). The threshold of stimulation which evoked locomotory movements varied from 0.1 to 0.3 V for different fish and for both monopolar and bipolar stimulation.

When the electrodes were 1–2 mm lateral to the midline, rhythmic movements occurred with the body tonically bent toward the side being stimulated.

DISCUSSION

Our results show it is possible to produce locomotory movements in skipjack tuna by the electrical stimulation of the midbrain. We feel that these evoked locomotory movements are "natural" for the following reasons. One, based on the position of the electrodes, it is highly unlikely that we are directly stimulating neurones within the spinal cord. Therefore, the activated neurones (or axons) within the "locomotory center" must be giving the command to swim to the spinal cord, which is the normal situation in teleosts (Grillner and Kashin, '76). Two, the induced tail-beat frequency was generally 5–6 Hz, which would result in a swimming speed of approximately three to four body-lengths per second in free-swimming skipjack tuna (Brill and Dizon, '79). These speeds are often maintained by free-swimming skipjack tuna (Magnuson, '78). Three, it is improbable that under our experimental conditions tuna can learn new unusual ways of swimming.

As was shown in previous work (Kashin et al., '74), the induced swimming movements of *Hexagnammus octogrammus* with implanted chrome electrodes were identical to those of intact fish. Ideally, to prove our hypothesis, we should show that midbrain stimulation is able to induce normal locomotion in free-swimming fish. This is not possible with skipjack tuna, because they must swim continuously to ram-ventilate their gills; and they quickly become hypoxic when their forward locomotion is interrupted.

We feel we have shown that midbrain stimulation in skipjack tuna is a viable alternative for creating normal locomotory activity that can be controlled by the experimentalist. Moreover, the fish used in this study survived and responded to brain stimulation for up to 6 hours. Our technique should therefore allow the biomechanics and energetics of tuna locomotion to be studied in a more controllable situation than is possible in a freely behaving fish.

ACKNOWLEDGMENTS

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8128

The Fish of the Month

Last March, Captain Carl Burlesci of the trawler *Colintino Rose II* made an educated guess: that waters near Point Sur on the mid-California coast would likely have a concentration of shortbelly rockfish. And right he was. In five days of fishing the vessel picked up nearly 75 tons in 14 tows.

But why would Burlesci go after this non-commercially-important fish? The answer is that his boat was under charter by the National Marine Fisheries Service (NMFS) to check out the practical details of a potential shortbelly rockfish fishery—to find out what would be appropriate gear and fishing strategy, what the catch and by-catch rates would be, and to help test on-board handling, shoreside handling, and marketing.

The shortbelly (*Sebastes jordani*) is quite atypical of fishes in the rockfish family, having a rather streamlined body and a deeply forked tail. Its curious name comes from the fact that its anus is located near the middle of the belly and not, like other rockfish, further back at the base of the anal fin.

It is a fast-growing fish, attaining sexual maturity at an average age of two years when the length is around 6½ inches, according to biologist Bill Lenarz of NMFS's Tiburon Laboratory. A 10-inch fish, the average size to be expected in a commercial fishery, weighs about one-third pound. Twelve inches is the largest fish commonly found.

The largest fish are always females. They carry developing embryos from January through March. Like other rockfish, shortbellies give birth to larval fishes instead of dropping eggs in the sea.

The diet of shortbelly rockfish consists primarily of krill (euphausiid shrimps), but the shortbellies no doubt also feed opportunistically on any prey of appropriate size. Studies by Tony Chess, another Tiburon biologist, indicate that shortbelly rockfish prefer canyons and drop-offs—areas where krill also congregate. The fish form compact schools during the day and usually, but not always, disperse at night when they feed.

For a fish that isn't commercially important, shortbelly rockfish is one of the better-known species to the

The *Colintino Rose II*, moored in Monterey harbor.

Checking Out Shortbelly Rockfish
Colintino Rose II's
Mission Accomplished

Article and Photos by Sus Kato

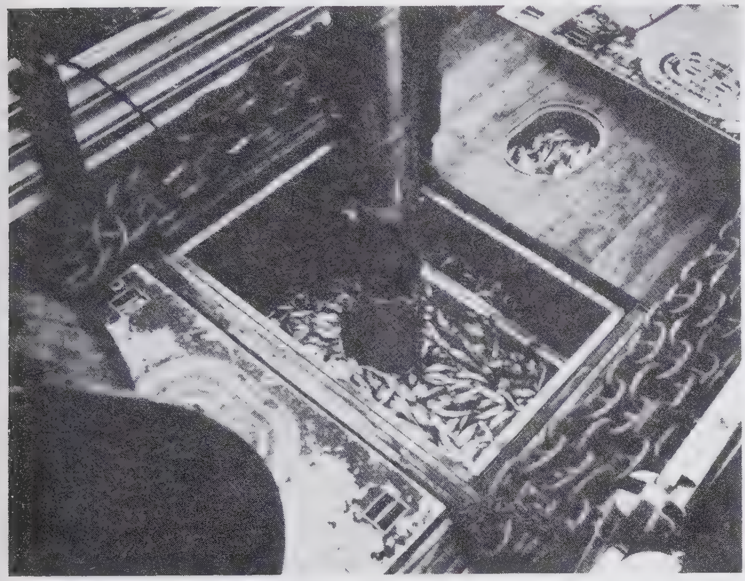
West Coast fishing industry, but they have rarely been caught in large numbers because they can easily escape through the 4½-inch mesh trawls used by California fishermen. Further, when they are caught, they are sometimes misidentified as juvenile bocaccio or chilipepper. And even when correctly identified, the small sizes of most shortbellies make them seem difficult to market.

But if the hoped-for expansion of U.S. fisheries is to take place, the potential of species like shortbelly rockfish must be given an all-out try. That's why NMFS chartered the *Colintino Rose II*, an 80-foot trawler from Fort Bragg, CA., and one of the vessels built after passage of the Magnuson Act with an eye toward new fisheries, to conduct a shortbelly-fishing experiment.

The crew of the *Colintino Rose II*, Captain Burlesci plus crew members Jeff Owens and John Savage, had had one season's experience in mid-water trawling for Pacific whiting and widow (brown) rockfish. They used the same gear to catch shortbelly rockfish, a No. 8 (three-quarters) Polish rope wing trawl. The entire 60-foot cod-end was lined with 1½-inch mesh webbing. A 1,000-pound weight was hung at each lower wing of the trawl. The doors were five square-meter Suberkrub midwater doors. A sonar unit, a fathometer with a CRT (cathode ray tube) display (which indicated strength of signals), a track plotter and a headrope transducer all made aimed trawling practical

Top:
Captain Carl Burlesci on the bridge with all the electronic aids used by modern trawlers.

Bottom:
A clean tow of 15,000 pounds of shortbelly rockfish being hauled up the stern ramp.



and efficient.

The *Colintino Rose II* left the Tiburon Laboratory's dock on March 17, and carried out a search pattern in 75 to 150 fathoms from San Francisco southward to Santa Cruz. Shortbelly had been consistently found in large numbers in this area in earlier research cruises. This time only one large shortbelly school was found, however, and a test tow revealed that the fish were small. That's when Burlesci, who had fished handline for rock cod in Monterey for several years prior to moving north and beginning to drag, recalled his earlier days and surmised that Point Sur might be a smart place to try.

The men found school after school of shortbelly there in 75 to 90 fathoms, some close to the bottom and others in mid-depths. In the five days of fishing starting on March 19, they caught 10,700 pounds in an average tow and their largest catch was around 15,000 pounds in a 40-minute tow. Their average length of towing time, once the net was in fishing position near the bottom, was 41 minutes. Towing speed was usually under 3 knots. Several times it was clear that a larger cod-end, or a small-mesh intermediate, would have yielded considerably more fish, as they saw trails of shortbelly spilling out through the 4¾-inch mesh of the intermediate, just in front of the cod-end.

They hauled the net aboard and opened it directly into the hold. For large catches, they separated the detachable front of the cod-end from the body so that fish spilled into the hold from both ends. Seventy-nine percent of the shortbellies caught were females, averaging 9.8 inches, while the males were smaller, averaging 8.7 inches. Many of the large females were gravid, carrying eyed larvae nearly ready to hatch.

As impressive as the catches of shortbelly were, even better were the low amounts of by-catches of other species. Only about 2,000 pounds of chilipepper and 1,000 pounds of bocaccio, the rockfish species of most concern to local fishermen, turned up in the net. This by-catch amounts to about two percent of the shortbelly catch. And, nearly all the incidentally caught rockfish were large enough for filleting, with juveniles virtually absent.

One tow produced about 4,000 pounds of widow rockfish along with an equal amount of shortbelly, but after studying the fathometer paper, Captain Burlesci concluded that schools of widows could usually be distinguished from those of shortbelly. No other widow rockfish were caught in subsequent tows.

The only other significant by-catch was about 350 pounds of small to large Pacific whiting caught in a night tow along with five tons of shortbelly.

The total catch of all other species (Pacific mackerel, market squid, sunfish, ling cod, midshipmen) was small, well under 100 pounds for the entire cruise. No salmon were taken at all.

The *Colintino Rose II* fishermen iced the catches made early in the day or during the first day of 2-day trips, but they simply dumped the later catches into the hold or on deck without refrigeration, to be iced immediately upon off-loading. With a fish pump, the vessel could be unloaded in less than 2 hours.

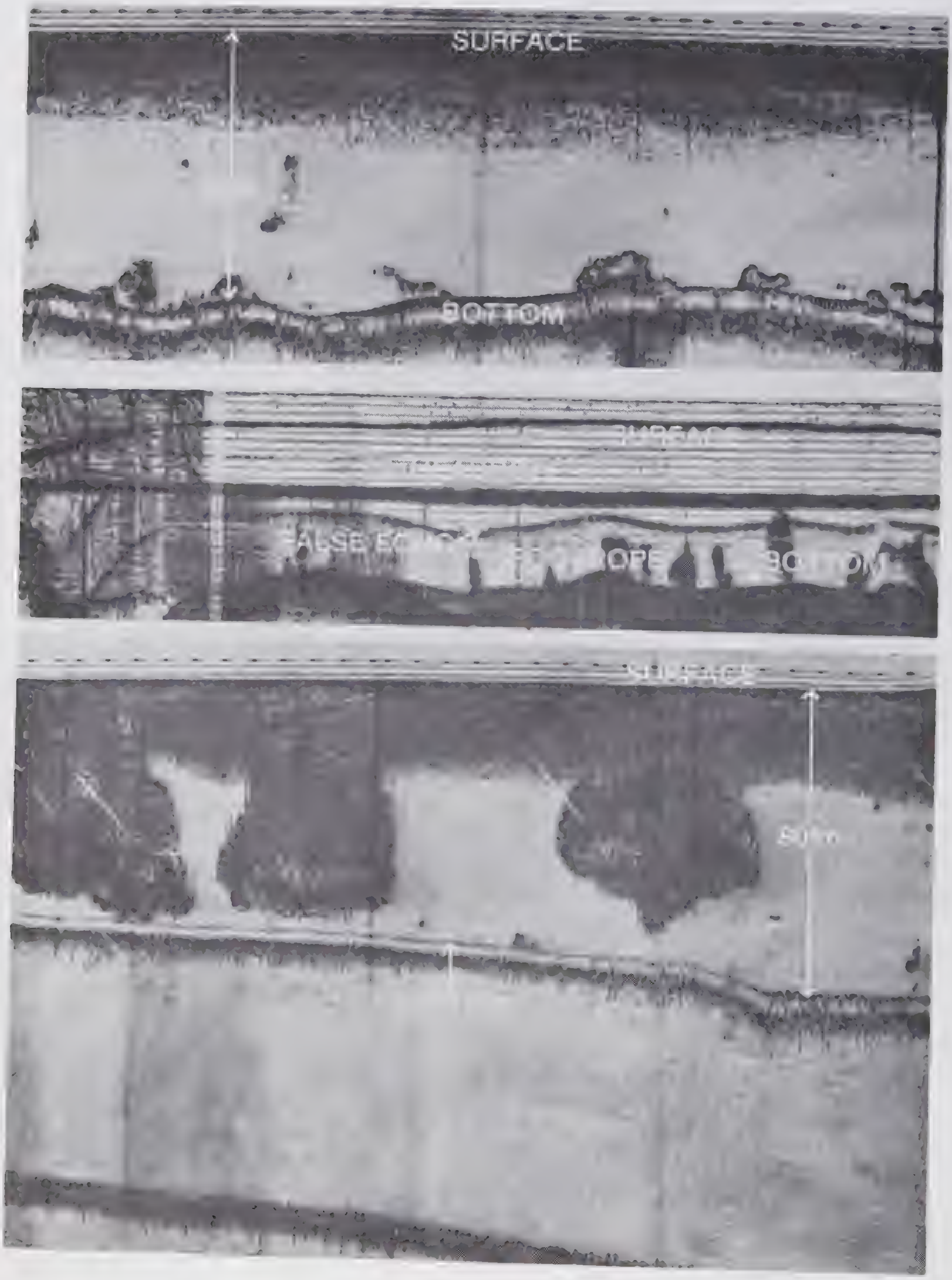
Next, Royal Seafood Inc. of Monterey and Producers Seafood of Oakland packed and froze the whole shortbellies in 22- to 30-pound cartons. These cartons then went into the hands of three other firms which would ship the shortbellies to Japan and do extensive market analyses. One firm shipped 20 tons to Japan, another shipped 7 tons and the third shipped a small amount.

All three firms reached similar conclusions, according to Shig Ohgami (San Francisco Trading Co., Oakland), Paul Wherland (International Multifoods, Minneapolis) and Yoshio Terajima (K.Y. Trading Co., Tokyo): that shortbellies have good taste, texture and appearance, and that they are suitable for traditional Japanese dishes such as fish cooked in soy sauce-based stock, fish served

Top Left:
Fish wells filled with shortbelly rockfish are unloaded with a suction pump.

Top Right:
Echo sounder marks (top half of photo) of shortbelly rockfish schools; in the lower half, the same fish are shown entering the trawl on the net monitor recorder.

Bottom Right:
Three large schools of shortbelly rockfish in midwater.


SURFACE
BOTTOM
SURFACE
FALSE ECHO
BOTTOM ROPE
BOTTOM
SURFACE
50 m

Shortbelly were packed and frozen whole in cartons lined with plastic.

raw, pickled, fried or broiled, or marinated in soybean paste (*miso*) and sweet wine (*mirin*), or boiled in seaweed stock.

There were also negative findings: that the small size of the fish is a detriment because of low meat yield; that it is not good as a dried or semi-dried product because of its small girth and lack of fat (however, one firm thought dried shortbelly has possibilities); that *surimi* made from fresh samples lacked elastic and binding properties (though this may have been due to lack of freshness or presence of parasites, or both, since nearly all white-fleshed fish have some degree of these properties); and that samples provided to the firms were of mixed quality, with varying fish sizes, spotty preservation and low fat content.

Long-term promotional efforts, the firms concluded, will be needed to move large amounts of shortbelly in Japan.

One of the three firms has now abandoned its shortbelly development efforts, but the other two are still pursuing possible avenues for shortbelly use. One firm sent samples to Africa, where the reaction was generally good but the price offered too low.

High freight costs probably make shortbelly an uneconomical product for U.S. processors, even if production costs are minimized. Samples were, however, sent to Baader North America Corp. in Massachusetts for trial machine-processing. Eydfinn Tausen of Baader reports that the best speed obtainable, using a herring machine, was only 90 fish per minute for a headed, gutted and filleted product. The yield of flesh was 40 percent, and "butterfly" fillets (skin-on) produced better results than conventional fillets. Baader found problems in aligning the fishes' heads correctly and in complete removal of guts.

If the shortbelly rockfish can be marketed whole at a decent price, the fishery could start quickly because local processors experienced in bulk-freezing whole herring have facilities to handle a substantial catch. Needless to say, local processors and fishermen are eager for the day when the large shortbelly resource can be put to use.

Fishing trials on the *Colintino Rose II* indicate that 15 to 20 tons can be caught daily in 3 or 4 tows. If the fishing areas were close to a landing port, daily trips could be made. At present, it is thought that the most likely area of concentration of shortbelly is about 20 miles offshore between Pigeon Point and Pillar Point (37° 10′ to 37° 30′ N.).

What questions remain? One is how to determine whether a particular school of shortbelly consists of small or large fish. Although the fish seem to segregate by size, schools of small and large fish are sometimes present in the same area, making it impossible to avoid catching small fish. It will be tempting for fishery managers to use mesh size limitations to save small fish, but this will cause problems with "gilling" to the point that fishing will be severely hampered.

Another question is how to handle the large amounts that can be taken in a single tow. Aboard the *Colintino Rose II*, it was difficult to handle very large amounts on deck. A lot of fish got crushed. On-board handling methods in general can stand much improvement.

At the plant, it is important to do a top-notch job of keeping the fish on ice until they are packed and frozen. Otherwise their pleasing color quickly fades, particularly if fresh water is too liberally used during washing and deicing operations.

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INDUCED SPAWNING OF A TUNA, *EUTHYNNUS AFFINIS*

Investigations into the biology of young tuna have been hampered by the difficulty of capturing and maintaining live larvae or early juveniles from the wild. The production of young in captivity would provide an obvious solution; however, the inherent difficulties of maintaining and working with such powerful, fast-swimming, pelagic fishes under conditions of close confinement have discouraged attempts to artificially stimulate their spawning. The following describes what we believe to be the first induced spawning of any tuna, accomplished with specimens of *Euthynnus affinis*, one of the smaller sized of the true tunas (taxonomic relations of tunas were recently reviewed by Collette (1978)). These were held captive in tanks at the Kewalo Research Facility of the Southwest Fisheries Center, Honolulu Laboratory, National Marine Fisheries Service, NOAA.

The specimens used in these spawning trials were three females in captivity for 2-4 wk and three males in captivity for about 4 mo. All were captured by hook and line and transported to the laboratory in the baitwells of either a commercial fishing vessel or the NOAA Ship *Townsend Cromwell*. They were maintained outdoors in circular, 7.3 m in diameter by 1.1 m deep tanks with water flow of about 3.0-3.5 l/s and temperatures ranging from 23.3° to 26.2° C. They were fed thawed surf smelt, *Hypomesus pretiosus*, and squid *Loligo opalescens* at a rate of about 15-20% of their body weight per day.

Sex and gonadal maturation of each specimen were determined by biopsy, with samples obtained by catheterization through the urogenital aperture (Shehadeh et al. 1973). While the fish were physically restrained for the biopsies, each was marked with an identifying numeral or letter with silver nitrate (Thomas 1975). Males in advanced stages of maturation could be recognized by the presence of milt in the catheter, while females in any stage of maturation could be identified from the biopsied ovarian tissue. The diameters of 25 ova of the largest size class present in the catheterized sample were measured with an ocular micrometer and the average diameter calculated as an index of ovarian maturation.

Gonadal maturation of captive specimens was monitored by monthly biopsies, starting in March 1979 with 37 specimens maintained since the preceding January and February. After March, newly captured specimens were also biopsied on the day of delivery to the laboratory. The most advanced ovaries in our captive fish between March and August 1979 were in three females delivered to the laboratory on 6 June. Their largest ova averaged 0.54, 0.48, and 0.44 mm on arrival and 0.55, 0.53, and 0.50 mm, respectively, when biopsied again 2 wk later on 19 June. The first two (females A and B, Table 1) were used in the first spawning trial, which started that same day, on 19 June. The third female (female C, Table 1) was biopsied again after an additional 2 wk, and its largest ova had increased to an average diameter of 0.56 mm. It was used in the second spawning trial, which started that same day, on 2 July. Males from groups captured earlier in January and February were also biopsied on the starting dates of the spawning

TABLE 1.—Spawning responses of *Euthynnus affinis* to treatment with salmon pituitaries (SP), human chorionic gonadotropin (HCG), and pregnant mare serum (PMS). Ova sizes represent mean diameters of 25 spawned ova after preservation in 3-5% Formalin,[1] or the largest size class in fresh biopsied samples.

	Day 1			Day 2			Day 3		
	Ova (mm)			Ova (mm)			Ova (mm)		
Specimen	Mean	SD	Treatment	Mean	SD	Treatment	Mean	SD	Response
Trial 1:									
Female A	0.53	0.03	SP 5 mg HCG 100 IU	0.54	0.04	SP 5 mg HCG 100 IU PMS 1,000 IU	0.55	0.04	Did not spawn.
Female B	0.55	0.05	SP 10 mg HCG 500 IU	0.57	0.04	SP 10 mg HCG 500 IU PMS 2,000 IU	0.77 0.98	0.02 0.02	Spawned (>35,000 released spontaneously; <10,000 stripped and fertilized).
Male A			HCG 100 IU			HCG 100 IU			No hydration of milt.
Male B			HCG 500 IU			HCG 500 IU			Hydration of milt.
Trial 2:									
Female C	0.56	0.03	SP 10 mg HCG 500 IU	0.70	0.04	SP 10 mg HCG 1,000 IU PMS 2,000 IU	0.78 1.02	0.03 0.03	Spawned (>185,000 released spontaneously; >40,000 stripped and fertilized)
Male C			HCG 1,000 IU			HCG 1,000 IU PMS 1,000 IU			Hydration of milt.

[1] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

trials, and specimens yielding milt in the catheter were selected. The selected males and females were transferred to a spawning tank identical in dimensions to the holding tanks but with water depth reduced to 0.61 m. Two females and two males were used in the first trial, and one female and one male in the second. Their sizes ranged from 47.0 to 52.9 cm fork length and 2.25 to 3.04 kg.

Hormone treatments administered were modified after those used by Leong (1977) to spawn Pacific mackerel, *Scomber japonicus*. Combinations of triturated, acetone-dried salmon pituitary glands (SP), human chorionic gonadotropin (HCG), and pregnant mare serum gonadotropin (PMS) were injected into the dorsal musculature with tuberculin syringes and 24-gage needles. The hormone preparations were suspended or dissolved in physiological saline and administered in injection volumes of 0.10-0.50 ml (Table 1). Each treatment consisted of two series of injections 24 h apart, starting at 2 p.m. in the first trial and 6 p.m. in the second. Responses of females were monitored by ovarian biopsies taken immediately preceding each series of injections, and spawning was detected by the appearance of the buoyant, pelagic ova in plankton nets (egg strainers) placed in the outflow from the treatment tank. Responses of males were based on subjective evaluation of hydration of milt, on the basis of whether milt could be expressed by moderate stripping pressure, and the fluid consistency of the milt obtained.

In the first trial, neither female showed any significant increases in sizes of largest ova within 24 h after the first injections (Table 1). However, ova were found in the strainers the next morning at about 8:15, about 19 h after the second injections. Biopsy of both females indicated that ovulation had been induced only in the one treated with higher dosages; similarly, examination of both males indicated that milt could be expressed only from the individual treated with the higher dosages. Eggs and milt were stripped from the responsive pair to effect fertilization. Most of the ova from this spawning were not viable and sank when placed in seawater, and of those that remained buoyant none progressed beyond early cleavage stages. This poor viability was probably caused by our failure to detect or respond to this induced ovulation early enough, with a consequent deterioration of the ovulated eggs within the ovarian lumen (Stevens 1966).

In the second trial, biopsy of the female indicated that its largest ova had increased in mean diameter from the original 0.56 to 0.70 mm within 24 h after the first injections. Ova were found in the strainer at 5:30 the next morning, 12.5 h following the second injections. Milt could be easily expressed from the male at this time, and the pair were stripped to effect fertilization. At incubation temperatures which ranged between 21° and 26° C, the first cleavage divisions were observed about 1 h after fertilization and the first hatching at about 31 h. With limited facilities for maintaining the developing embryos, we were able to sustain only a small fraction of the fertilized eggs obtained. About 300 larvae were hatched and they developed and absorbed their yolk sacs over 2 d. It was not our intent or purpose at this stage of these investigations to attempt to feed or rear these larvae, and they all died by the end of the third day.

Previous attempts to produce young tuna in captivity have been concentrated in Japan, and along two lines of effort. One is the fertilization at sea of ova obtained by stripping freshly captured, running-ripe fish (Yasutake et al. 1973; Harada 1978; Ueyanagi 1978). Since running-ripe females are only infrequently taken in current commercial fishing operations, these efforts have produced only occasional successes. The other approach is to maintain adult-sized specimens in large, netted enclosures in coastal waters with the hope that they will eventually start spawning naturally. (By coincidence, the first known spawning of a species of tuna in such a situation was reported to have occurred with bluefin tuna, *Thunnus thynnus*, on 20 June 1979 (Sōgō 1979) at the same time that our first induced spawning of *E. affinis* was taking place.) Whether either of these two approaches can be developed into reliable spawning operations for tunas remains to be determined. The two consecutive hormone-induced spawnings that we achieved with *E. affinis* suggest that this technique can be developed into a routine procedure, at least for this species. Work is expected to continue at the Honolulu Laboratory on refinement of effective treatments and to be initiated on rearing of the resultant larvae.

Acknowledgments

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OVERVIEW

PHYSIOLOGICAL ECOLOGY

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The second Early Life History of Fish Symposium in April 1979 brought together scientists from all over the world who have dedicated their efforts to answering questions on how fish eggs and larvae are adapted to their environment, and how this adaptation has insured species survival. In this, the largest section of the Symposium volume, a wide variety of species, habitats and physiological functions are reported on. The field of Physiological Ecology, encompassing as it does such a diversity of organisms, has only in recent years been focussed so extensively on the eggs and larvae of fishes. Scientists such as Blaxter, Hempel, Holliday, Ahlstrom and Rollefsen, to name a few, gave impetus to these investigations during the 1950's and 1960's. Since then, as evidenced by the large number of papers which follow in this volume, interest has grown enormously in this specialized subject. We attribute this to two reasons: (1) the newly found ability to apply information on fish eggs and larvae to fisheries and aquaculture problems; and (2) the academic interest in survival of fish species. There has been a flood of ideas on the use and usefulness of fish larvae in investigations of fundamental properties of populations such as recruitment, natural mortality and genetics. Studies of physiological ecology contribute to improved understanding of the recruitment process by sorting out the relative importance of the influence of single and multiple environmental variables on larval fish survival including hydrostatic pressure (Atlantic herring), salinity (mullet), light (porgy, sculpin), temperature (grunion), oxygen (northern anchovy), temperature and salinity (Baltic herring, cisco, whitefish, and roach), and dissolved oxygen and bottom-type (salmon). Other more holistic studies relate results of experiments on laboratory larvae reared under differing prey concentrations to simulated or actual conditions in the ocean. Results are reported on studies on Engraulidae, Soleidae and Sparidae from coastal waters of Florida, and anchovy from two pelagic ecosystems: the southern anchovy, *Engraulis ringens*, off the coast of Peru and the northern anchovy, *E. mordax*, off the California coast. In both studies an important key to larval survival and recruitment lies in obtaining improved measurements of *in situ* concentrations of larvae and coincident patches of their prey. This work can only be carried out successfully where the hydrography of the region is adequately described. In this context the northern anchovy model comes closest to providing a basis for developing a predictive index of recruitment. It is important to note that the study represents the combined efforts of a multiyear, multidisciplinary laboratory-field study of the recruitment process in a pelagic ecosystem.

New information on the effects of changing prey densities on larval growth and survival based on laboratory studies is reported for the Atlantic herring, cod, and haddock. This approach is a necessary precursor to testable hypotheses in microscale studies of fish larvae and their prey on the continental shelf. The possible role played by density dependent regulatory mechanisms in limiting the size of marine fish populations is elaborated in predator-prey studies of two or more species. Preliminary insights are contained in the reports for Atlantic mackerel, Pacific mackerel, bigeye anchovy, haddock, smelt, lake trout, anchovy, Atlantic herring and sprat, Argentinian scianids, and a nearshore fish community in Japan.

An important measurement in fisheries ecosystem studies is the general health or "condition" of fish eggs and larvae. Significant advances have been made in the past 6 years for measuring "condition". The need for obtaining a reliable measure of condition is particularly acute in estimating impacts of pollution on the viability of exposed ichthyoplankton. Several investigators have used otoliths successfully (norther anchovy, northern lampfish, silversides, souther anchovy, grunts, and Atlantic mackerel Morphometric and histological criteria have als proven useful for assessing a condition-factor fo Pacific mackerel, northern anchovy and spot. I reports given to other sessions, two promising ne approaches to measuring physiological conditio include the use of DNA/RNA ratios of larval fis protein (Systematics and Development section) an the application of cytogenetic techniques to determin morbidity levels in fish eggs and larvae (Pollutio section).

The following section provides us with a look at th future, as well as the recent past, in this field. We ca expect to see a continuing growth of research on fis eggs and larvae and exciting results on the physiological ecology during the next decade, judgin from the number of people currently involved, th wealth of problems being attacked, and the problem still to be solved.

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FACTORS CONTRIBUTING TO VARIABLE RECRUITMENT OF THE NORTHERN ANCHOVY (*ENGRAULIS MORDAX*) IN THE CALIFORNIA CURRENT: CONTRASTING YEARS, 1975 THROUGH 1978

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Studies on the distribution of first-feeding larval anchovy and their food were made to test the hypothesis that the upper mixed layer of the ocean must be in a stable (non-turbulent) state for survival of enough larval anchovy to insure the production of a good year-class. Turbulent conditions destroy food aggregations and dilute potential food organisms to below feeding threshold concentrations of first-feeding larval anchovies. Surveys during the anchovy spawning season of 1975, 1976, and 1978 provided data supporting this hypothesis. Food of first-feeding larval anchovies became limiting when storms (1978) or drastic upwelling (1975) occurred which diluted food aggregations. A complicating factor was that nutritionally inadequate larval fish food could be occasionally overwhelmingly dominant in the larva's environment (1975). The drought year (1976) was characterized by stable conditions in the Southern California Bight and produced one of the best of the last 16 anchovy year-classes; 1975 produced one of the worst. Partial success of the anchovy year-class in 1978 is predicted based on the onset of stable conditions and food aggregations in the latter part of the spawning season.

INTRODUCTION

THE STOCK AND RECRUITMENT PROBLEM[1]

In recent years the stock and recruitment problem has become an active area of investigation as part of fishery studies throughout the world; of particular interest to fishery scientists are ways to predict future fish year-class sizes and how to determine the causes of the huge variability often seen in year-classes which cannot be ascribed to the size of the spawning stock. In the last decade work toward elucidating these mechanisms has been based chiefly on Hjort's (1914) suggestion that the strength of a year-class of fishes is most probably established through differential larval mortality during the earliest larval feeding stages and is dependent upon the amount and kind of food

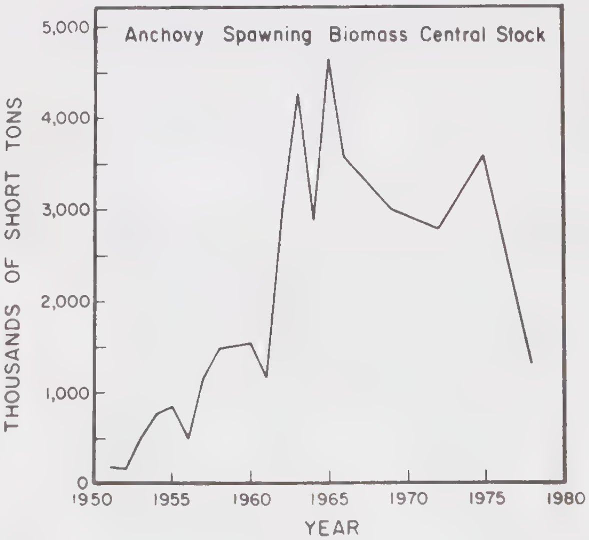

Figure 1. Variation in Northern anchovy biomass with time. Data provided by Dr Paul E. Smith.

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[1] Briefly stated, the following questions are asked: 'What are the major factors controlling reproduction and larval survival, and what is the impact of reduced stock size on the strength of future recruitment into a year-class?' Figure 1 shows the wide fluctuation in spawning biomass of the Northern anchovy that can occur even in adjacent years.

available to the larvae when they first begin to feed. Other hypotheses have been suggested; for example, predators may have a great depressant effect on larval populations because early larvae are particularly vulnerable to a variety of vertebrate and invertebrate predators (see Hunter, 1976). With respect to food and predators, Lasker and Smith (1977) concluded that "survival of larvae appears to be related to coincidence rather than abundance alone; that is, a patch of larvae will survive if it coincides with an adequate patch of food organisms and also if it does not coincide with a patch of predators adequate to destroy the larval patch."

In recent years, correlative techniques have established relationships between physical and chemical factors in the environment and the strength of various fish year-classes, e.g., Pacific mackerel (Parrish and MacCall, 1978; Parrish et al., in press) and Atlantic menhaden (Nelson et al., 1977), but even these are usually explained by indirect effects on larval survival, e.g., larval drift into good or poor feeding areas. Density dependency, i.e., on the average, the larger the stock the greater the resulting year-class, is also considered to be a viable hypothesis by many fishery scientists.

TEST OF HJORT'S HYPOTHESIS

In 1975 I presented results of field experiments which indicated that Hjort's (1914) hypothesis might be tested by establishing the threshold number of particles needed for feeding by a larval fish, by determining the vertical and horizontal distribution of suitable food particles in the larva's environment, and by monitoring the temporal and spatial changes that occur in larval food concentrations, eventually correlating these with the resultant year-class (Lasker, 1975).

Although the "threshold-for-feeding" idea was tested only for the larval anchovy (*Engraulis mordax*), it may be applicable to other fishes for which it can be determined that a minimum concentration of food is needed for the larvae to feed and survive. Not all areas of the ocean can supply the required levels of food for all fish larvae, and I showed (Lasker, 1975) that in the Southern California Bight, anchovy larvae are dependent for survival mainly upon the inshore environment for an above-threshold number of nutritious particles. Offshore areas were seen to be particularly sparse in the kinds and sizes of particles needed by first-feeding larval anchovy. I suggested that storms might be an important mechanism for disrupting larval food aggregations, because in April 1974 after a storm I recorded a dramatic reduction in chlorophyll (Fig. 2) and potential larval fish food particles per unit volume.

An extensive survey of the Northern anchovy's environment was made in 1975 and the results were reported recently (Lasker, 1978). These suggested that strong upwelling, when it occurred during the anchovy spawning season, could be destructive to the establishment of a new year-class because it disrupted aggregations of suitable food particles and caused dilution of the particles to concentrations below the threshold needed by larval anchovy for first feeding.

Another important factor in survival of first-feeding anchovy larvae was suggested by Lasker et al. (1970) and confirmed by Scura and Jerde (1977) when they showed that the particles eaten by the anchovy larva and usually represented by dinoflagellates or microzooplankton of various kinds, were not always nutritionally complete. Above-threshold numbers of food organisms usually appeared when dinoflagellates were in bloom proportions or when they were other aggregating mechanisms (e.g., diurnal migration) which permitted particle number per unit volume to exceed the threshold for larval anchovy feeding. If the

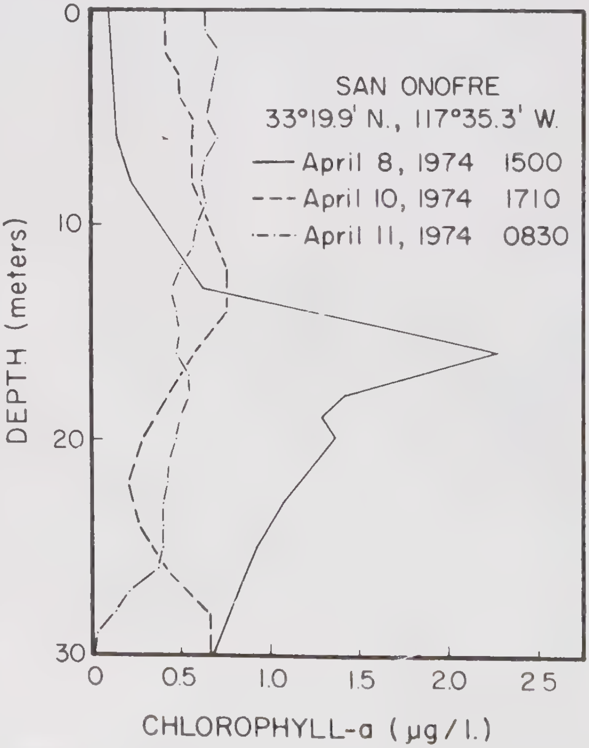

Figure 2. Reduction in chlorophyll before and after a storm. A major contributor to the chlorophyll maximum on 8 April was the dinoflagellate *Gymnodinium splendens*, (after Lasker, 1975).

dominant particle was nutritionally inadequate and also the chief food source for the larva, then a large mortality might be expected. This was suggested (Lasker, 1978) when the dominant particle in the larval anchovy's environment during the 1975 spawning season was found to be the dinoflagellate, *Gonyaulax polyedra*, and which Scura and Jerde (1977) showed to be an inadequate food for survival and growth of first-feeding anchovy larvae.

Upwelling brings nutrients to the surface and results in high levels of primary productivity in the surface layers of the sea and particularly in water adjacent to the shore. This is a common course of events in the Southern California Bight but enhanced productivity does not necessarily ensure good larval fish feeding conditions despite the fact that above-threshold-for-feeding concentrations of particles, usually a variety of diatoms, are prevalent during these events. Behaviorally, the anchovy larva ignores or rejects diatoms, probably because diatoms are spiny and filamentous. These phytoplankters are rarely found in the anchovy larva's intestinal contents (Arthur, 1976; Berner, 1959; Scura and Jerde, 1977).

TEST OF THE "STABILITY" HYPOTHESIS

In early 1978, California experienced unusual climatic conditions during the winter months. Storms were frequent and intense: precipitation in Southern California set a 20-year record, e.g., San Diego experienced 56 cm (22 inches) of rain as opposed to the 100-year average of 25 cm (10 inches). In this paper I present the results of an oceanographic survey made in the Southern California Bight during the stormy year of 1978 and compare the distribution of larval anchovy food with that found in 1975, a year of relative calm but also characterized by a geographically extensive upwelling along the coast in the midst of the anchovy spawning season. From the temporal and spatial descriptions of the Southern California Bight in 1975 and 1978 and with additional data from 1976, I draw conclusions on the hypothesis I have proposed, that stability of the ocean's upper layers during the anchovy spawning season is essential for larval fish food aggregation, a prime requisite for larval anchovy survival and thus a successful year-class. Readers are referred to my recent paper (Lasker, 1978) for details on the anchovy fishery and the methods employed in obtaining the information on oceanographic, meteorological and biotic conditions described in the following.

FLUCTUATIONS IN YEAR-CLASS STRENGTH OF THE NORTHERN ANCHOVY

There has been an active fishery on the Northern anchovy out of the California port of San Pedro for some years. The catch has been sampled and apportioned according to age and the percent year-class composition determined by the California Department of Fish and Game who have published their results in a series of articles (Collins, 1971; Collins and Spratt, 1969; Spratt, 1972, 1973; Sunada, 1975).[2] Table 1 indicates the percent composition of anchovy year-classes from the 1965 through 1977 seasons. The variability in strength of year-classes is quite evident. For example, the strong year-classes of 1970, 1971, and 1972 show up clearly as large percentages of the year-class composition in years succeeding the establishment of each year-class; by comparison, 1974 and 1975 were relatively poor. I anticipated a poor 1975 year-class because of the dominance of the dinoflagellate *Gonyaulax* as the major food particle in the larval anchovy's environment. Also the advent of strong upwelling during the latter half of the spawning season destroyed any food aggregations that might have been beneficial for feeding and prevented others from forming except inedible diatoms. As I pointed out earlier, the dinoflagellate *Gonyaulax polyedra* is known, from laboratory experiments (Scura and Jerde, 1977), to be a poor food for anchovy larvae. The 1976 year-class showed up very strongly in the fishery in 1977. This was earlier than any other "zero" group of northern anchovy since 1969. These fish were either born earlier or growth was extremely rapid after the usual spawning period.

Table 2 provides a ranking of the proportionate contribution of 16 Northern anchovy year-classes to the fishery off California. The 1975 year-class was one of the worst of this record while the 1976 year-class was one of the best. In this ranking, 1977 appears poorer than average. Data for 1978 is not available at this writing (January 1979), but the environmental data presented in this paper will provide the basis for a prediction of the relative future contribution of the 1978 year-class to the fishery. Notably, 1976 and 1977 were energetically quiet years off southern California, characterized by drought, high barometric pressure, no storms, and many cloudless days, and contrasted strongly with 1978, a very stormy year. This will be discussed in the next section.

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[2] Since the central subpopulation of the Northern anchovy straddles the U.S.-Mexico border, in recent years the Mexican fishery out of Ensenada, Baja California, has also been sampled and apportioned by age. Data for the 1976 and 1977 year-classes are from Sunada (pers. comm.).

Table 1. Percent composition of Northern anchovy year-classes in the commercial catch from 1965 to 1977. (Data provided by John Sunada, California Department of Fish and Game.)

	Age in years						
Season	0	I	II	III	IV	V	VI
1965–66	4.5	14.7	48.5	23.4	7.5	...	...
Year-class →	1965	1964	1963	1962	1961	1960	1959
1966–67	6.9	22.9	38.1	23.0	7.5	...	...
Year-class →	1966	1965	1964	1963	1962	1961	1960
1967–68	...	...	...	...	...	...	...
Year-class →	1967	1966	1965	1964	1963	1962	1961
1968–69	18.5	45.9	23.4	8.2	4.3	...	...
Year-class →	1968	1967	1966	1965	1964	1963	1962
1969–70	27.0	27.8	35.2	8.3	...	...	...
Year-class →	1969	1968	1967	1966	1965	1964	1963
1970–71	4.0	32.1	40.2	20.1	3.1	...	...
Year-class →	1970	1969	1968	1967	1966	1965	1964
1971–72	11.3	50.8	26.7	8.5	2.4	...	...
Year-class →	1971	1970	1969	1968	1967	1966	1965
1972–73	9.3	25.7	47.6	14.4	2.4	0.4	...
Year-class →	1972	1971	1970	1969	1968	1967	1966
1973–74	6.9	20.3	35.3	30.7	6.2	1.0	...
Year-class →	1973	1972	1971	1970	1969	1968	1967
1974–75	4.6	18.5	39.5	26.4	9.6	1.3	...
Year-class →	1974	1973	1972	1971	1970	1969	1968
1975–76	2.4	10.5	37.3	34.1	12.0	3.2	...
Year-class →	1975	1974	1973	1972	1971	1970	1969
1976–77	27.7	12.1	16.2	27.8	13.4	2.5	...
Year-class →	1976	1975	1974	1973	1972	1971	1970
1977–78	10.6	37.7	20.3	14.0	14.0	2.4	0.2
Year-class →	1977	1976	1975	1974	1973	1972	1971

THE OCEAN ENVIRONMENT

TEMPERATURE, SALINITY AND UPWELLING

In 1975, surface temperatures in January, February and March were about a degree cooler than the 1950–78 mean of 14.7°C in the Southern California Bight and the adjacent California Current. In fact, a large pool of 13° to 14°C water extended from Pt. Conception to Baja California and over 100 km seaward. Salinity was close to the long-term mean of about 33.5 °/oo . Conditions were drastically different in 1978. Storms and heavy precipitation characterized December 1977 through mid-March 1978. Salinity was extremely low, 33.2 – 33.3 °/oo , over the entire area for the first 3 months of 1978. This may not be entirely explained by precipitation and run-off, although this may have been the dominant factor (McLain et al., 1979, R. Lynn, pers. comm.). Surface temperatures were much warmer than normal in 1978; nearly 16° C in January and 15° to 16° C in March, 1° C above the long-term mean (Eber, 1977). Bakun (1973, 1975) has published upwelling indices for the entire west coast of the United States. Upwelling indices are values of Ekman transport derived from atmospheric pressure differences and are expressed in cubic meters of upwelled water per second per 100 m of coastline. Figure 3 shows upwelling indexes for January 1977 to March 1978 compared with a 32-year (1946–77) time series. Locations in the Gulf of Alaska are toward the top of the figure, while those off Baja California are toward the bottom. Note that the stormy period from December 1977 through mid-March 1978 coincided

Table 2. Northern anchovy year-classes are ranked by using the annual deviation from the mean of the proportionate contribution of each anchovy year-class to the fishery (Paul E. Smith, personal communication).

Year-class	Rank	Year-class	Rank
1962	5	1971	8
1963	3	1972	6
1964	12	1973	10
1965	13	1974	14
1966	15	1975	16
1967	4	1976	1
1968	9	1977	11
1969	7		
1970	2		

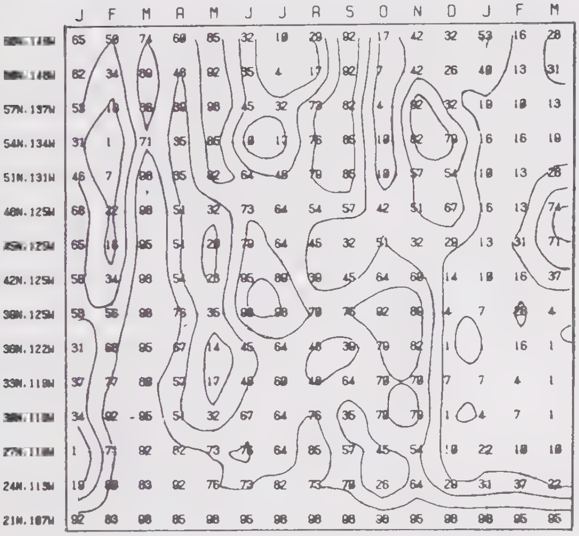

Figure 3. Monthly upwelling index values for January 1977 to March 1978, in percentiles of the frequency distribution made up of the 32 values for each month and location in a 32-year (1946–77) time series. Locations in the Gulf of Alaska are toward the top of the figure; those off Baja California are toward the bottom. The contour interval is 25 percentiles. Values above the 50th percentile indicate stronger than normal upwelling while those below indicate weaker than normal upwelling (A. Bakun, personal communication).

with very low upwelling index values from as far north as 39° N, 125° W to as far south as 27° N, 116° W, i.e., from Cape Mendocino to Vizcaino bay, California, a distance of 1600 km. This encompasses the area of Northern anchovy central subpopulation spawning (Vrooman and Smith, 1971).

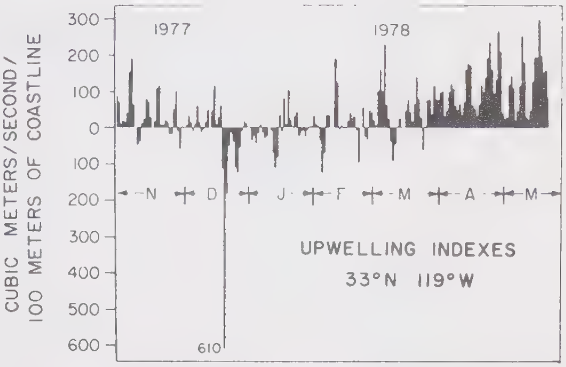

Figure 4. Upwelling index at San Clemente Island approximately 65 miles off the southern California coast and indicative of oceanographic events in the Southern California Bight. The major downwelling response in December 1977 was due to a violent storm. Other downwelling episodes are indications of additional stormy periods. Note their virtual cessation by mid-March 1978.

WINDS OVER THE ANCHOVY'S SPAWNING GROUNDS

In 1975, wind from the north (southward) early in the year was much more frequent and prolonged than in early 1978 and resulted in intense upwelling. While there was a major storm pulse in the first few days of March 1975, storms were much more frequent and intense in 1978, as evidenced by frequent and intense northward winds and the concomitant decrease in southward winds. The strongest initial stormy event was very evident in the San Diego area as illustrated by a major downwelling pulse shown in Bakun's indexes for 33° N 119° W (Fig. 4). This mid-December 1977 event presaged turbulent conditions in the mixed layer of the Southern California Bight which persisted and were maintained by successive stormy events through most of the 1978 anchovy spawning season until mid-March.

Because of the importance of both upwelling and storms to the disruption and dilution of larval anchovy food aggregations, a quantitative analysis of wind was investigated as a possible simple way to characterize the energy available to induce turbulence in the upper mixed layer of the ocean. In Table 3, the mean cube of the wind speed, which is roughly proportional to the mechanical energy available for inducing turbulent mixing (Niiler and Krause, 1977; Elsberry and Garwood, 1978) for two locations (central California coast north of Pt. Conception: 36° N 122° W and San Clemente Island; 33° N 119° W), is presented. While there is not a perfect coherence between the two

Table 3. Mean cube of the wind speed over four spawning seasons (1974–75 to 1977–78) of the Northern anchovy. 36° N, 122° W is representative of the California coast north of Pt. Conception; 33° N, 119° W of the Southern California Bight.

	Mean cube of the wind speed at 36° N 122° W					
Spawning season	Dec	Jan	Feb	Mar	Apr	Dec–Feb Average
1974–75	416	274	534	756	538	408
1975–76	232	132	186	495	644	183
1976–77	42	110	121	539	580	91
1977–78	583	621	375	334	230	526

	Mean cube of the wind speed at 33° N 119° W					
	Dec	Jan	Feb	Mar	Apr	Dec–Feb Average
1974–75	281	314	300	598	529	298
1975–76	250	185	280	661	603	238
1976–77	90	220	266	622	644	192
1977–78	413	192	267	338	391	291

locations, the similarities are apparent and consistent. For example, 1976 and 1977 were much less windy years than 1975 and 1978, particularly when averages of wind cubed for December through February are compared. The highest wind cubed index of the 1977–78 series at 33° N 119° W was in December 1977, a particularly stormy month. Winds at 36° N 112° W, when compared to previous years, were also exceptionally strong in December 1977.

An analysis of these wind events suggests the following: (1) winters of the drought years 1975–76 and 1976–77, when anchovies were spawning, were characterized by much lower cumulative wind speed cubed over the Southern California Bight, the chief spawning ground of the Northern anchovy; and (2) the winter of late 1977 and early 1978 was characterized by unusually strong storm winds, which were potentially disruptive to stratification in the upper mixed layer of the Southern California Bight.

To summarize, the winters of 1976–77 and 1975–76 were consistently relaxed, low-energy situations while the winter of 1977–78 was marked by intense, highly fluctuating northward wind stress episodes. The winter of 1974–75 was relatively high in cumulative southward wind energy although upwelling did not commence strongly in the Southern California Bight until mid-February.

BIOLOGICAL CONSEQUENCES OF UNUSUALLY STORMY CONDITIONS IN THE SOUTHERN CALIFORNIA BIGHT

TEMPORAL AND SPATIAL SPAWNING DISTRIBUTION OF THE NORTHERN ANCHOVY, 1978

Figure 5 shows the seasonal and seaward distribution of first-feeding anchovy larvae found in the Southern California Bight over the 1978 spawning season, as indicated from plankton tows taken along

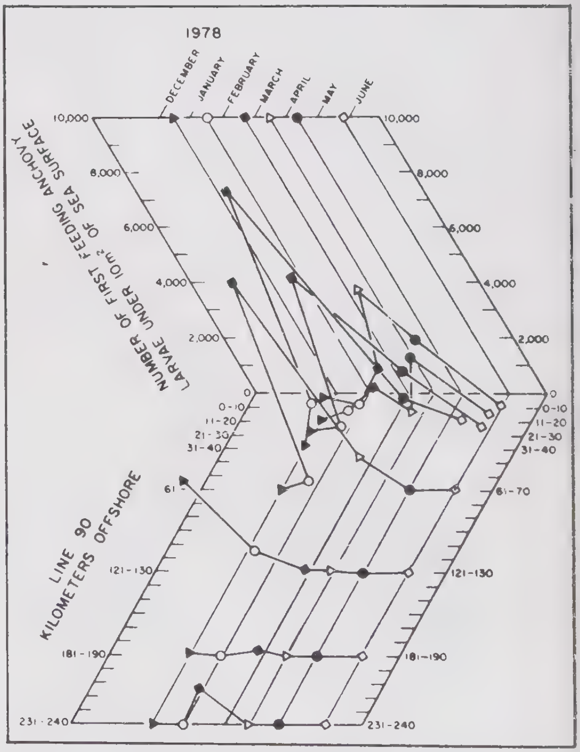

Figure 5. First-feeding larvae under 10 m² of sea surface plotted by distance from shore and time from December 1977 through June 1978 for CalCOFI line 90. Refer to Figure 9 for geographic locations of CalCOFI lines.

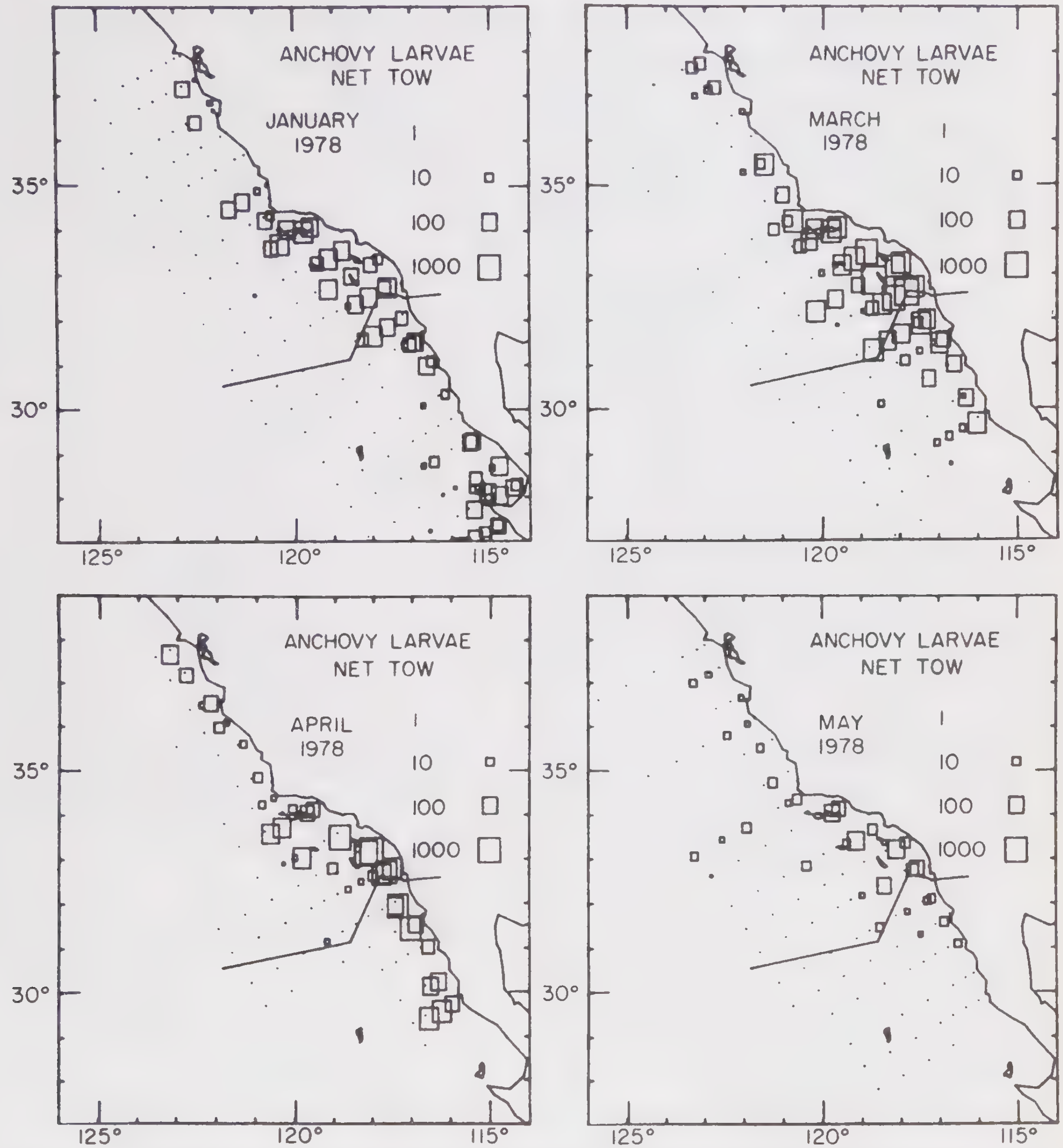

Figure 6. Larval anchovy distribution during the 1978 spawning season. Each dot indicates an occupied but "zero larvae" station. The line extending from land is the Mexico-U. S. border. (Graphs courtesy of Dr Paul E. Smith).

CalCOFI line 90[3]. An interesting feature of this graph is the comparatively low number of larvae which appeared inshore during January, February, and March. Figure 6 shows that anchovy spawning was extensive throughout the Southern California Bight during the entire season but was minimal offshore.

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[3] Geographic locations of sampling transect lines are shown in Figure 8.

THRESHOLD PARTICLE CONCENTRATIONS FOR FIRST-FEEDING ANCHOVY LARVAE

Lasker (1975) determined that between 14° to 15°C, 30–40 particles per ml, are needed in the larval anchovy's local environment to provide for gut filling in a reasonable time period (8 h). Confirmation of this threshold based on metabolic needs and prey capture efficiencies was given by Lasker and Zweifel (1978) where they simulated the percent survival of anchovy larvae after the first day of feeding in various concentrations of organisms at 14°C. From these results, it seems unlikely that the threshold for feeding can be as low as 20 particles per ml. However, in this study, because higher temperature decreases the threshold for feeding (Lasker, 1975) and slightly higher temperatures prevailed in the Southern California Bight in 1978, larval anchovy survival is discussed in terms of a threshold of 20 particles per ml for first feeding.

PARTICLE DISTRIBUTION WITH DISTANCE, DEPTH AND TIME IN THE SOUTHERN CALIFORNIA BIGHT

The number of particles per ml are plotted against time and distance from shore for the two major lines sampled (lines 87 and 90) during the California Cooperative Oceanic Fisheries Investigations (CalCOFI) cruises during the anchovy spawning season in 1978 (Fig. 7). Except for Santa Monica Bay (inshore stations, line 87), which had reasonably high numbers of 30–50 μm diameter particles before the major December 1977 storm, the entire Southern California Bight was literally devoid of food particles suitable for first-feeding larval anchovy during January, February, and early March. Stable conditions which became established in mid-March were reflected in bloom conditions of some organisms, particularly *Gymnodinium splendens*, a food known to be nutritious for first-feeding anchovy larvae (Fig. 8). Figure 8 also shows clearly that the storm event of December 20 (see Fig. 4) destroyed the aggregation of dinoflagellates which would have been good feeding for larval anchovies. In fact, it wasn't until March 13–18 that above-threshold-for-feeding concentrations of dinoflagellates began to appear at these inshore stations. Diatoms became more prevalent after this period of time but probably did not contribute to larval feeding success because, as noted before, these are not eaten by Northern anchovy larvae. The results of continued turbulence are also evident in low particle concentrations over the entire Southern California Bight recorded from December to March 1978; elevated particle concentrations show up in mid-March after general relaxation of stormy conditions (Fig. 9).

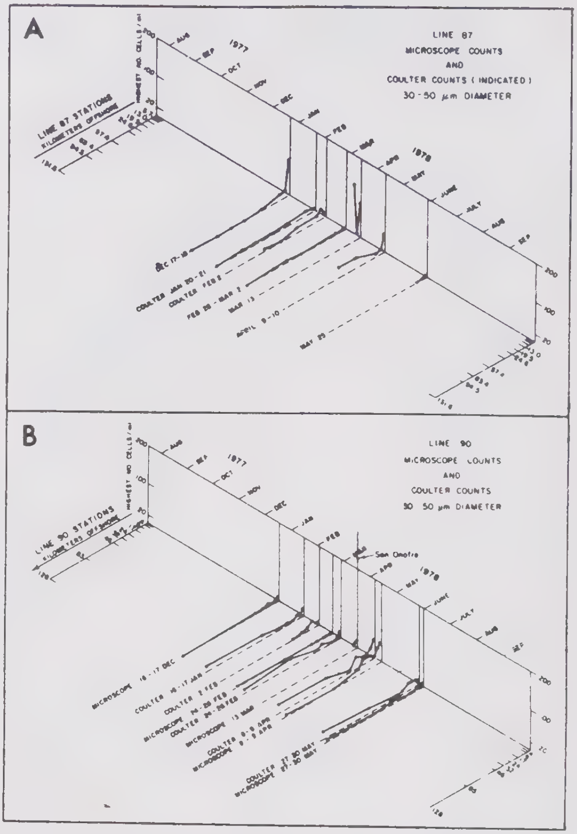

Figure 7. Particle distribution with time and distance from shore, lines 87 and 90. Refer to Figure 9 for geographic location. Note the depressed particle numbers below threshold for larval first-feeding until March at the inshore stations. The >200 particles/ml at San Onofre was a patch of *Gymnodinium splendens*.

A similar picture is seen in the distribution of chlorophyll along line 90 and shown in Figure 10. Whatever chlorophyll maximum layer existed on 16–17 December 1977, it was completely obliterated right after the major storm event and no reasonable quantity of chlorophyll appeared until late February in the most inshore stations. Chlorophyll was much more prevalent during the 8–9 April transect of the Bight and became layered in the following months, reflecting stable (i.e., non-turbulent) conditions. This indicates that storms kept the upper 30 m of the Southern California Bight well mixed and diluted with respect to particles but once storms ceased, recovery was relatively rapid and stratification of phytoplankton became firmly established by April. April spawning in the inshore zone was the highest of the year (Fig. 5) and despite poor conditons for larval

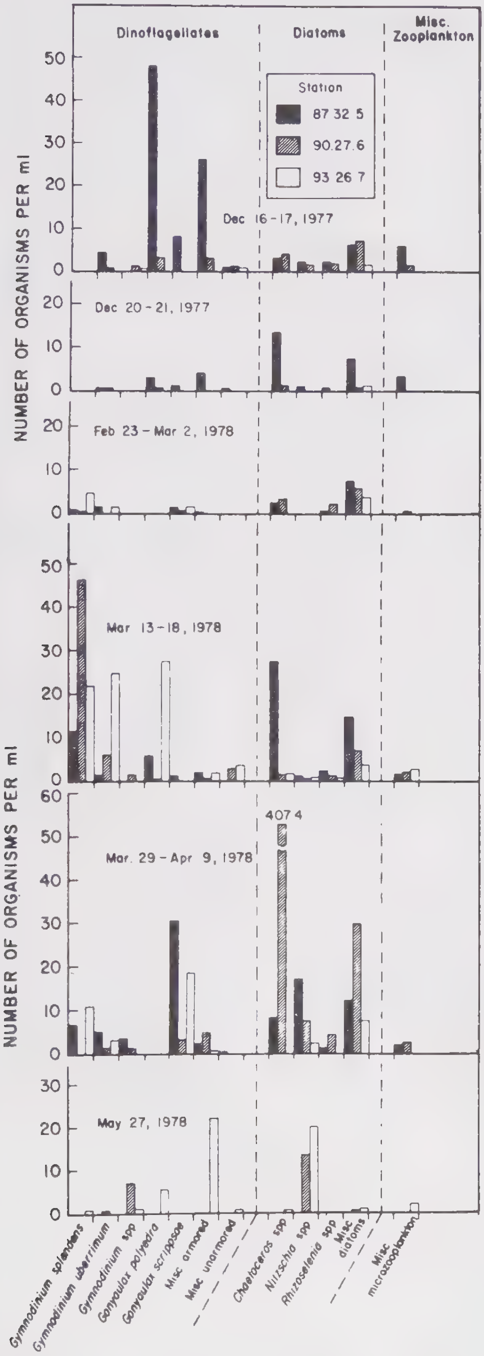

Figure 8. Diatoms, dinoflagellates and miscellaneous zooplankton >20 μm diameter at three inshore stations in the Southern California Bight. The storm of 20 December reduced aggregations well below larval anchovy first-feeding threshold levels (i.e., <20/ml).

anchovy survival during January, February, and early March, the stable conditions prevailing from mid-March through April probably avoided a failure of the 1978 year-class.

EVIDENCE OF DELAYED LARVAL ANCHOVY SURVIVAL, 1978

Two ancillary lines of evidence seem to indicate that the anchovy achieved a partial spawning success late in the 1978 spawning season. First of these is the appearance of small anchovies in schools in June and July, although these could not be caught by commercial fishermen because of their small size. The minimum size for fishing by regulation in the southern California area is 12.7 cm total length, although smaller fish are caught by bait dealers along the coast. Age structure of two samples of these small fish, as deduced from daily rings on their otoliths (Brothers et al., 1976), shows that most of them were born after mid-March (R. Methot, pers. comm.) (Fig. 11).

Second, a small bird, Xantus' murrelet (*Endomychura hypoleuca*), which nests on some of the Channel Islands off California, feeds heavily on late larvae of Northern anchovy. In 1976, clutch initiation started in early March and in 1977 in late March. In 1978, it was almost early May before clutch initiation started (Fig. 12). This suggests a lack of food for this highly specialized feeder, possibly due to a delay in the survival of anchovy larvae (G. Hunt, pers. comm.).

1976 AND 1977 SPAWNING SEASONS

Eggs and larval surveys were not conducted in 1976 and 1977, but, as noted earlier, the 1976 Northern anchovy year-class was one of the best of the 16 year-classes from 1961 through 1977. Reid et al. (1978) provide some information of phytoplankton aggregation in the Southern California Bight in 1976 which showed that there was strong vertical stability and a sharp chlorophyll maximum layer throughout the inshore areas of the Bight. The most significant taxa in the chlorophyll maximum layer were the dinoflagellate *Exuviella* sp. and the photosynthetic ciliate *Mesodinium rubrum*, both of a size easily seen and consumed by *E. mordax* first-feeding larvae. I conducted a survey of the Bight for threshold numbers of larval anchovy food organisms in March 1976 over the CalCOFI grid and the results (Fig. 13) showed above-threshold concentrations of particles, consistent with calm seas, prolonged stability and aggregation of motile phytoplankters. Reid et al. (1978) listed a wide variety of organisms which were found in the area and concluded that there were elongate bands of phytoplankton oriented parallel to the shore. My results show that concentrations of these organisms were highest inshore as well.

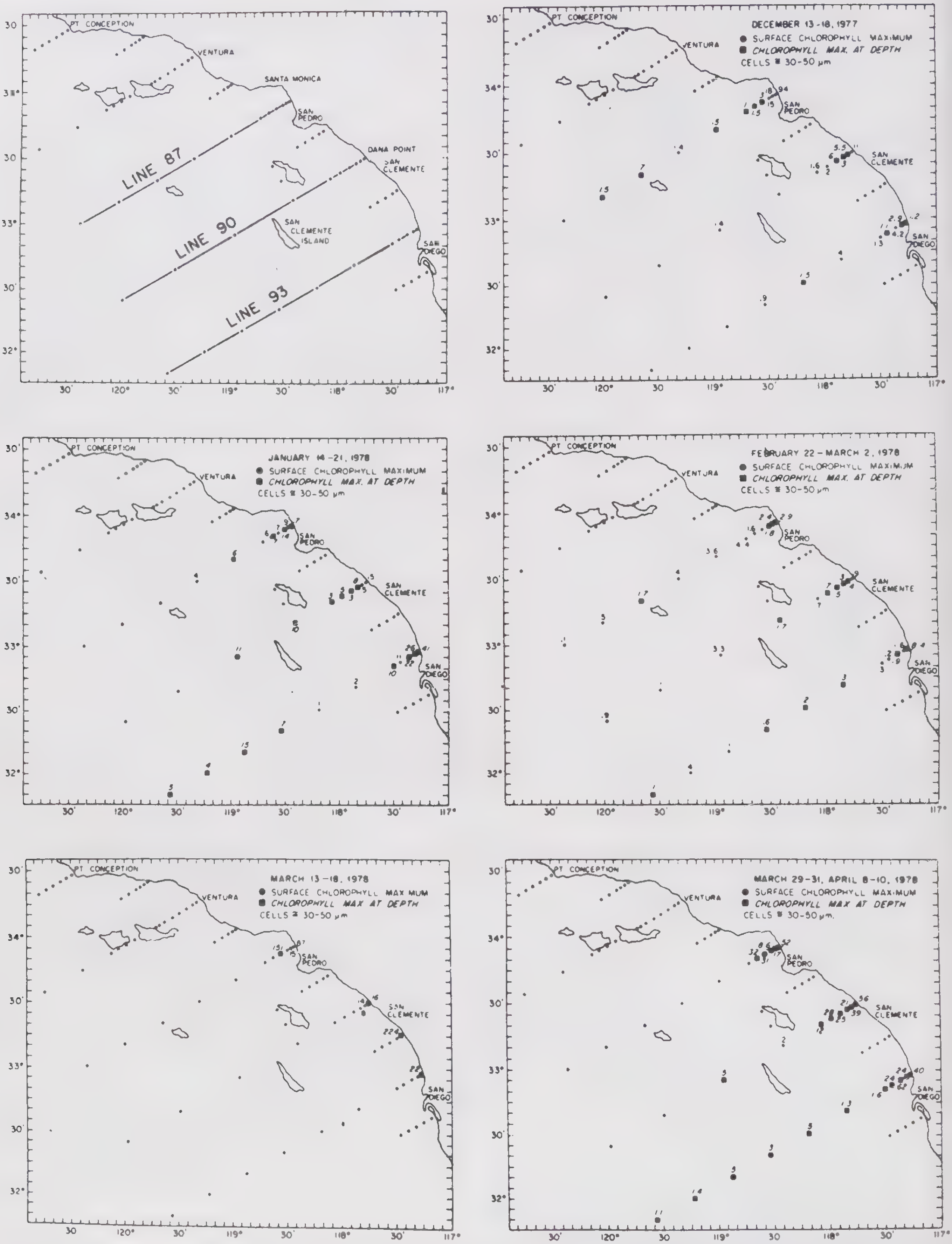

Figure 9. Particle distribution in the Southern California Bight during the 1978 anchovy spawning season. Numbers are cells per milliliter. Storms kept concentrations of particles in the 30–50 μm size range below threshold for larval anchovy first feeding. Calm conditions in mid-March presaged phytoplankton aggregations.

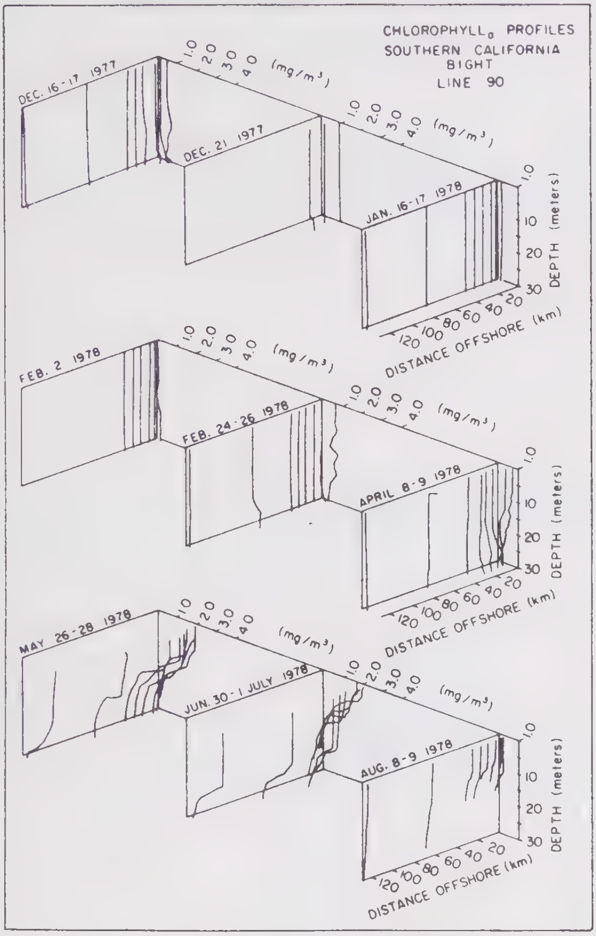

Figure 10. Vertical chlorophyll profiles with time and depth along line 90 (San Onofre, California) throughout the anchovy spawning season.

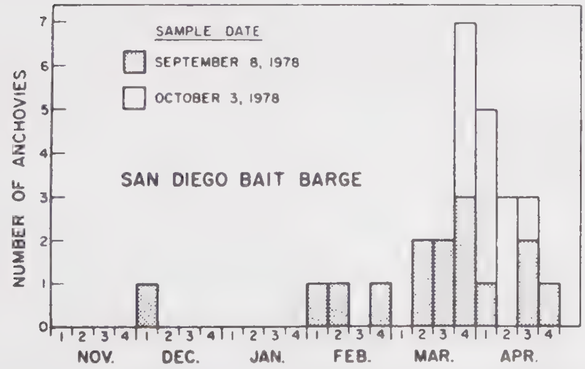

Figure 11. Birthweeks of pre-recruit anchovies caught in September and October 1978 (R. Methot, pers. comm.).

Figure 14 shows the results of particle counts in the 30–160 μm diameter range, taken on 16–17 March 1976 in a tight station pattern along shore from Encinitas, California to La Jolla, California, a distance of 15 km. A complete microscopic analysis of 10 samples from the chlorophyll maximum at the northernmost station showed that dinoflagellates were dominant, averaging 35 cells per ml, and *Exuviella* sp. constituted 68% of these. Copepod nauplii averaged 20 per liter and the globular dinoflagellate *Noctiluca* sp. numbered 54 cells per liter. Diatoms did not exceed 10 per ml. From what we know of the threshold concentrations of phytoplankton needed for larval anchovy first feeding (i.e., >20 cells/ml of dinoflagellates), March 1976 exemplified excellent feeding conditions. Unfortunately, no consistent sampling was possible in 1977 during the anchovy spawning season, so no clues are available to assess the 1977 year-class.

PRODUCTIVITY AND YEAR-CLASS STRENGTH

Cumulative productivity (data collected and analyzed by Dr Richard W. Eppley of Scripps Institution of Oceanography) is given in Figure 15 for the Southern California Bight from 1974 through 1978. The poor anchovy year-class of 1975 corresponded with a generally elevated productivity in the Bight, undoubtedly brought about by the extensive upwelling that year. This was also reflected in chlorophyll measurements taken at the same time by Lasker (1978). The year of the very good year-class, 1976, was a relatively poor one for primary production in the Bight. My interpretation of these events is that primary productivity *per se* is less essential to larval survival than prolonged stability of the upper mixed layer (no upwelling, no storms) which allows for aggregation by vertical and horizontal migration of motile larval anchovy food organisms, probably dinoflagellates. Stability also provides conditions conducive to the deliberate hunting-feeding behavior of the larval anchovy. High production is usually also indicative of diatom production, which is not a favorable condition for successful feeding by first-feeding anchovy larvae.

DISCUSSION

This study, with others (Lasker, 1975, 1978), has shown that food of first-feeding larval anchovies becomes limiting when storms or drastic upwelling occurs and dilutes food aggregations. A complicating factor is that often nutritionally inadequately larval fish food can be overwhelmingly dominant in the

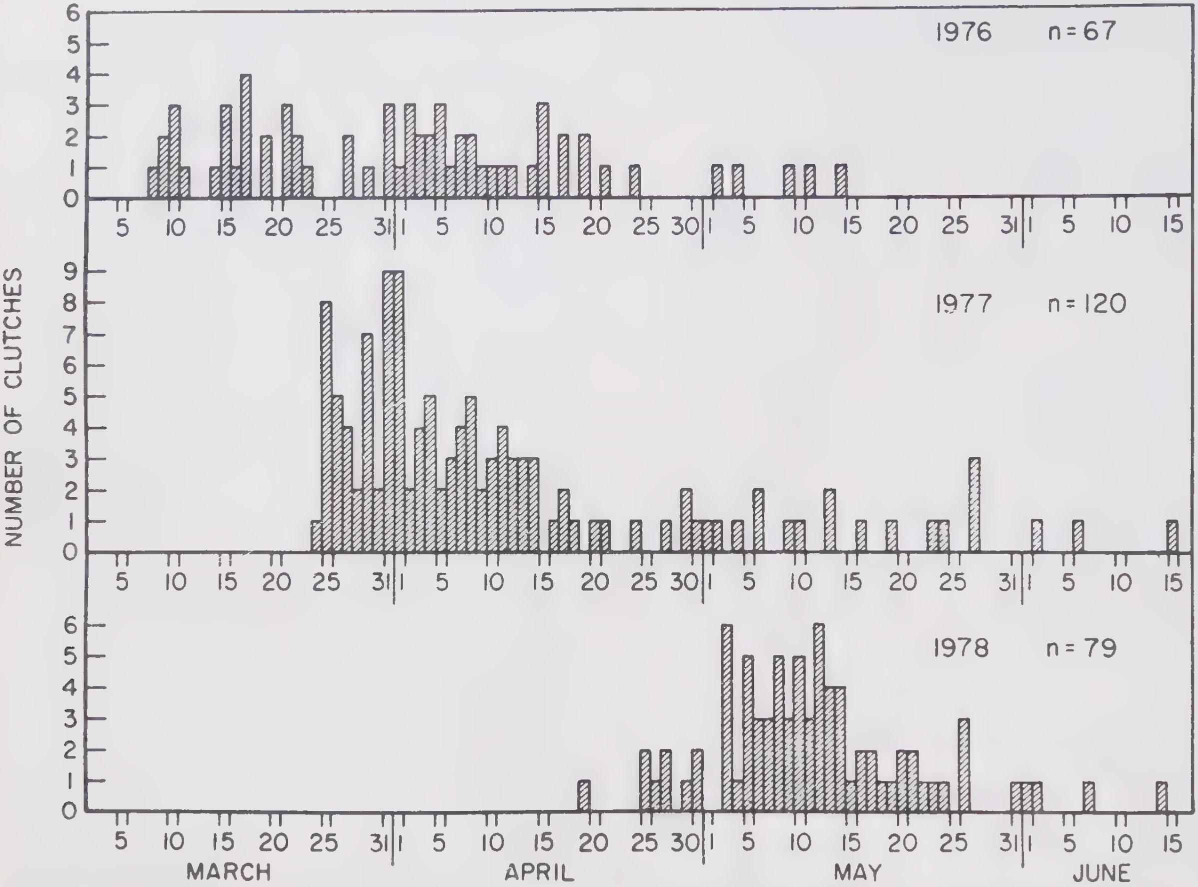

Figure 12. Clutch initiation dates (1976–78) for Xantus' murrelet (*Endomychura hypoleuca*) (G. Hunt, pers. comm.), nesting on Channel Islands in the Southern California Bight.

larva's environment despite otherwise favorable oceanographic conditions. Several conditions seem to be necessary for the survival of first-feeding anchovy larvae; these are stability of the water column and aggregation of nutritionally suitable food organisms coinciding with the production of anchovy larvae in time and space.

The years investigated and compared in this paper, 1975–78, provided interesting comparisons. In early 1975, the weather and seas of the Southern California Bight were relatively calm, but a nutritionally poor food organism, *Gonyaulax polyedra*, was the dominant one available to first-feeding anchovy larvae. Upwelling in the latter half of the spawning season swept out *G. polyedra* but replaced it with diatoms which the larvae do not eat. The result of these events was one of the poorest year-classes of anchovies in the last 16.

The drought year 1976 had calm seas and very little upwelling during the anchovy spawning season. Dinoflagellates were plentiful, diatoms were sparse, and stratification was strong. The resultant year-class was one of the best of the last 16. No data are available to assess the 1977 year-class.

In early 1978, southern California had one of the stormiest seasons on record. Stratification was nonexistent until March. A poorer-than-average year-class is expected because only a portion of the spawning season could have resulted in good survival. Early evidence is that most pre-recruits were born after March 1978.

Correlating year-class strength with oceanographic, meteorological and biological parameters that affect larvae requires a lag of 2 years between collection of environmental data and information on the magnitude of the resultant year-class as obtained from

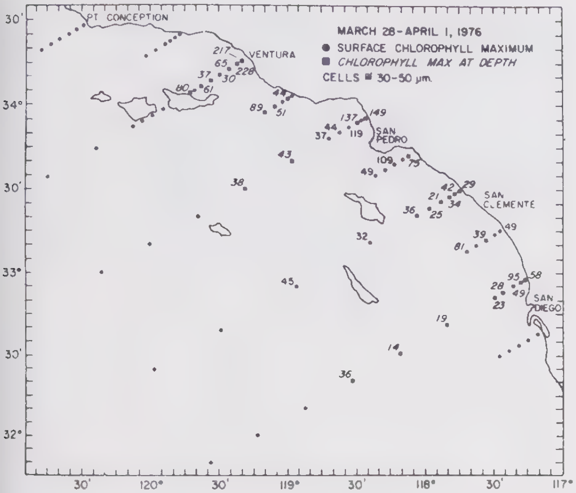

Figure 13. Particle distribution (30–50 μm) over the CalCOFI grid, March 1976. Numbers are cells per milliliter. Note the uniformly high particle concentrations during this period of calm and drought.

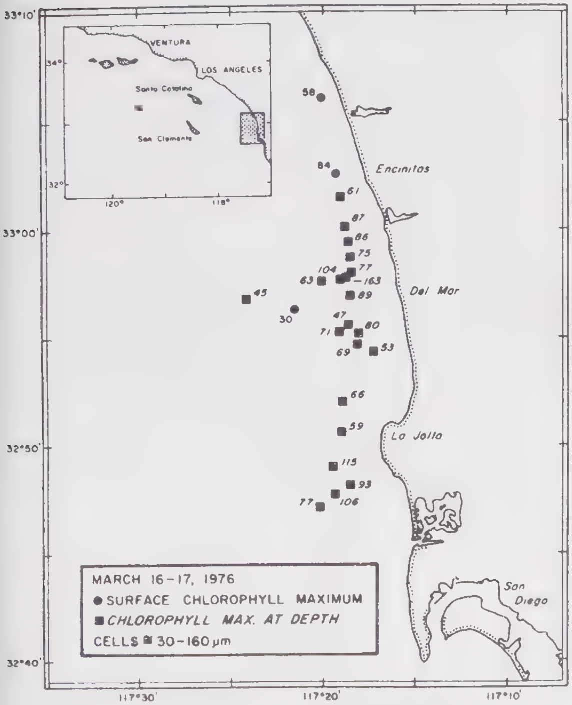

Figure 14. Particle distribution from an along-shore transect (30–160 μm), March 1976 in the Southern California Bight. Numbers are cells/milliliter.

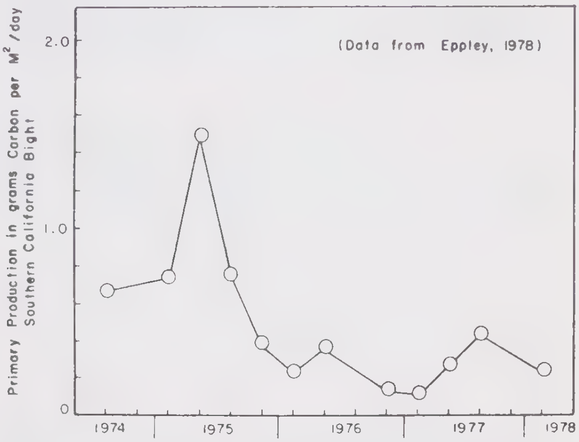

Figure 15. Cumulative carbon production of the Southern California Bight, 1974 through 1978 (R. Eppley, pers. comm.).

the fishery. The difficulty of this task precludes obtaining the statistics necessary to test the "stability" hypothesis vigorously in a short span of years, particularly with an annually spawning fish. The prediction of year-class strength probably depends on knowledge of wind stress, direction, duration, number of repeat episodes, and the depth of the ocean in which stress is translated into turbulence and mixing. The extent and speed of restratification after wind events is also important and is currently an active area of investigation (Garwood, 1977).

As far as larvae are concerned, the biotic components of their environment are equally as important for survival, e.g., the degree of patchiness of larvae, their food, and predators. However, if we can establish quantitatively the interactions suggested in this paper between weather, ocean, biota, and fishery, the results may give insights needed to understand the important relation between stock and recruitment, and provide the information needed to permit a prediction of the magnitude of an incoming year-class.

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The Role of a Stable Ocean in Larval Fish Survival and Subsequent Recruitment

Reuben Lasker

The Role of a Stable Ocean in Larval Fish Survival and Subsequent Recruitment

Pelagic fish populations can and do undergo precipitous and catastrophic recruitment failures. Peru suffered a massive collapse of its fishery for anchoveta, *Engraulis ringens* (Valdivia, 1978), resulting in a reduced catch from 1971 to 1973, i.e., from 12 million to 2 million tons, an economic disaster. Experts called in by the Food and Agriculture Organization of the United Nations and the government of Peru noted that the decline in the population of the Peruvian anchoveta had much in common with similar declines of other clupeoid species, e.g., the Atlanto-Scandian herring, the Pacific sardine, the Hokkaido herring, and the Japanese sardine (Murphy, 1974). They concluded that heavy fishing on a parent stock after the appearance of several poor year classes is sufficient to reduce the stock's reproductive potential to a point where it can no longer produce enough recruits for the fishery.

However, a very small population size did not prevent the recent resurgence in the fishery for the Japanese sardine, *Sardinops melanosticta*. This is a striking example of how a pelagic fish population can undergo a remarkable recruitment success. From 1964 to 1972, the Japanese sardine was virtually absent from local waters around Japan, but within five years (1973–1978) this fish increased steadily in numbers and now appears as a very large population around the home islands, particularly in local waters east of Honshu. The catch increased from a negligible one of a few thousand tons in 1972 to almost 1.64 million tons in 1978 (Fig. 1). Kondo (1980) attributed this increased catch to a single large year class which appeared *de novo* in 1972 and whose subsequent spawning successes from 1974 through 1977 provided the large tonnage of sardines to the fishery. Kondo believes that the breakdown of a long-established cold water cell adjacent to the coast permitted the Kuroshio Current to approach close to the home islands of Japan, that this led to an increase in the quantity of food available for larval fish (chiefly copepod nauplii), and resulted in enhanced larval survival with a subsequent increase in the sardine population.

The causes of natural large population changes cannot consistently be shown to be density dependent. The Japanese sardine is a good example of this. Its resurgence from extremely low population levels to one supporting a two-million-ton fishery in just a few years highlights anew the questions asked by fishery scientists: "To what extent can a pelagic stock be fished before subsequent year classes resulting from that stock are affected?" "At what

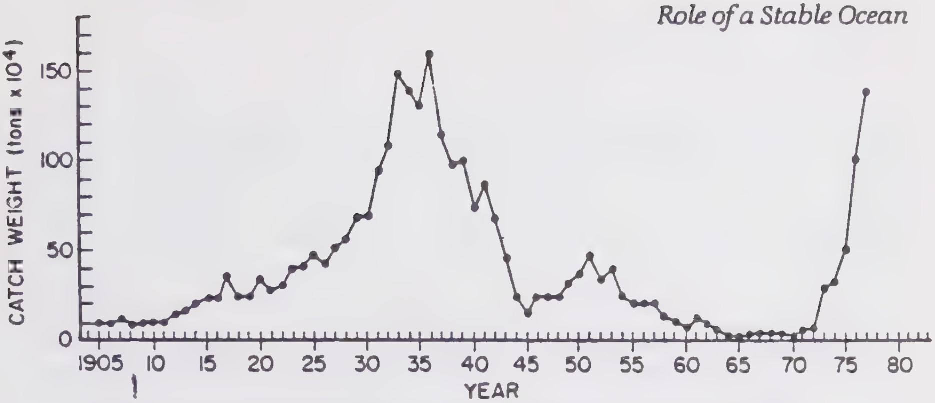

Figure 1. Fluctuation of the sardine catch around Japan (after Kondo, 1980).

population size of a fish can recruitment, the successful survival of fish from hatching to a size exploitable by a fishery, be shown to be density dependent, if at all?" Answers to these questions would help greatly in elucidating the relationship between stock and recruitment and ultimately the management of highly volatile pelagic stocks.

Over the past three decades, scientists have tried to find correlative physical, chemical, and biological ocean parameters which could be used to predict migration patterns, recruitment, and large fluctuations in population biomass—but with very limited success. The management of fish populations has marched apace, with decisions usually based on historical precedents but rarely on scientific principles. Yet the collapses of recruitment-limited fish populations have had enormous economic and social effects on fishing nations. These might have been avoided had there been reasonable predictions on the fate of the fish populations due to fishing and the environment.

The vastness of the ocean and the difficulty of sampling spatially and temporally present major problems to fisheries scientists. Fisheries managers would like useful "real time" information, but it is not uncommon to have to wait a year or longer to obtain data, process them, and reduce them to an interpretable form. Long delays in assessing the strength of incoming year classes introduce great uncertainties about future recruitment. Furthermore, most clupeoids recruit into the fishery from one to two years after they are born, accounting for a built-in delay. Statistics on cohorts, age, growth, and relative mortality must wait at least for the fish to grow up and be caught by the fishery. Predictions based on catch statistics are frequently too late to be useful, and the mechanisms determining the amount of future recruitment are not elucidated at all by a study of the catch.

Johan Hjort's Hypothesis of the Larval Fish Critical Period

While there have been a number of suggestions for investigating the stock and recruitment problem, in recent years scientists have tended toward the belief that vulnerable early life stages of pelagic fish hold some important clues to understanding large variations in recruitment. This idea is not new. In 1914 the eminent Norwegian fishery biologist, Johan Hjort, suggested that year classes of the Atlanto-Scandian herring, *Clupea harengus*, fluctuate in magnitude according to the availability of food to its very earliest larval stages. He hypothesized that resultant year classes are small when food is scarce and large when food is abundant. Although Hjort had no direct measurements to support his idea, scientists find it attractive even today, although supporting evidence is still mostly inferential and speculative. After a 60-year hiatus, Hjort's idea has been resurrected and elaborated upon, and evidence has been and is being accumulated from the ocean and the laboratory to test its basic tenets.

Does a Good Year Class Depend on a Stable Ocean and Good Food?

In California at the National Marine Fisheries Service, Southwest Fisheries Center (SWFC), La Jolla, Lasker and his coworkers have developed an extension of the Hjort hypothesis which accepts the initial premise that food for first-feeding larvae may be limited but suggests that there are times and places in the sea where food aggregation occurs and that survival of larvae depends on these. Lasker (1975) describes the use of laboratory-produced first-feeding anchovy larvae to detect good feeding areas in the sea and to establish the threshold concentrations for feeding by the larva. The importance of a stable environment for feeding was demonstrated in these experiments, and at the time of this study the nearshore less-turbulent environment was shown to be better for larval anchovy feeding than offshore in the mainstream of the California Current. Cruises in late 1974 and 1975 (Lasker, 1978) revealed a 300-kilometer-long by 4-kilometer-wide patch of the thecate dinoflagellate, *Gonyaulax polyedra*, along the southern California coast in December and its extension to 40 kilometers wide in January. While present in concentrations above the threshold for feeding during these two months, *G. polyedra* also was demonstrated to be a poor food for anchovy larvae (Scura and Jerde, 1977). A massive upwelling along the coast in February 1975 wiped out the patch and reduced particle concentrations far below threshold-for-feeding by first-feeding anchovy larvae.

In addition to food density, survival of fish larvae also depends on particle size and species composition of food organisms (Lasker et al., 1970; Scura and Jerde, 1977). For instance, in March–April 1974 the naked dinoflagellate *Gymnodinium splendens* was the dominant food particle in the larva's environment and was known to be nutritious and desirable (Lasker et al., 1970). Thus species succession, particularly after upwelling periods, may result in the replacement of desirable food organisms (e.g., some species of dinoflagellates) with undesirable ones (e.g., diatoms), once again resulting in poor larval feeding conditions despite the fact that primary production may be high.

The 1975 spawning season of the northern anchovy can be summed up as follows: (1) *Gonyaulax polyedra*, a thecate dinoflagellate but a very poor food, dominated the first-feeding larva's environment; (2) an upwelling occurred late in the spawning season which swept out this poor food, but no suitable food appeared in its place; (3) 1975 produced one of the worst northern anchovy year classes on record.

To test these ideas further, Lasker and Zweifel (1978) produced a simulation model, based on laboratory and field data, of survival and growth of first-day-of-feeding anchovy larvae, *Engraulis mordax*, on different prey sizes and concentrations. They showed that at nominal capture efficiencies of 20–30 percent, there is a threshold of 30–50 small particles (45–55 μm diameter) per milliliter needed for substantial survival and growth. Large particles, e.g., copepod nauplii (95–105 μm diameter), can enhance survival when they are in concentrations of between 10 and 100 per liter, but the same environment must contain above-threshold numbers of small particles. This simulation showed an important distinction between survival and average growth; i.e., larvae may survive in significant numbers in feeding regimes in which the *average* growth for the population is negative. The concept relating larval fish food aggregation to stability of the water column and its relation to oceanographic and meteorological conditions needs to be tested in a variety of habitats.

Vlymen (1977) showed the importance of the geometry of prey distribution in his study of the larval anchovy in physical relation to its food. In particular, his simulation model indicated that extremely different larval anchovy growth rates in the sea are the most likely functions of prey contagion, with the highest growth rates not necessarily occurring at the highest level of prey contagion. Owen (in press) sampled within chlorophyll maximum layers on a vertical scale only 20 cm apart and found significant differences in numbers of potential larval fish food organisms, often between adjacent 20 cm water samples. This seems to confirm Vlymen's contention that the centimeter scale of aggregation must exist in the sea and that it occurs for every food type yet identified as needed for larval anchovy growth and survival.

Larval fish drift and the conditions which cause it are further elaborations of the Hjort hypothesis. Some scientists believe that upwelling events, if strong enough, can carry fish larvae out of good feeding areas into poor ones. At the California coast, when upwelling is weak, the stable environment inshore results in good feeding for young fish and enhanced survival. Working with fishery statistics on Pacific mackerel (*Scomber japonicus*) year-class strength, an upwelling index (Bakun, 1973), and a wind curl index (Bakun and Nelson, 1977), Parrish (1976) and Parrish and MacCall (1978) have shown good correlations of upwelling, surface transport patterns, and year-class strength of Pacific mackerel off California.

On the east coast of the United States, Nelson et al. (1977) showed that menhaden larvae, which depend on estuaries for food, are carried into estuaries during downwelling periods. In this case, upwelling acts to the detriment of larval survival by keeping larvae offshore, a mechanism different from the disruption of food aggregations shown to be important for northern anchovy larvae.

Storms also were found to disrupt larval food aggregations, and it has been inferred that this probably results in heavy larval mortality during the anchovy spawning season (Lasker, 1975). A regional cube-of-the-wind-speed index for the anchovy spawning grounds off California has been developed by Andrew Bakun at the Pacific Environmental Group (SWFC) of the National Marine Fisheries Service and used by Lasker (in press) to correlate with good and poor anchovy year classes.

While the data are still sparse, indications are that an index of this kind, which reflects the amount of mechanical energy available for stirring the upper layers of the ocean (Niiler and Krause, 1977), may be a valuable predictor of poor feeding conditions of larvae and hence the degree of recruitment. For example, a violent mid-December 1977 storm in southern California destroyed layers of potential larval anchovy food; stability was not restored to the upper layers of the inshore anchovy spawning region until March. Lasker, at the 1978 CalCOFI Conference, suggested that unusual storm conditions during winter 1977–78 would adversely affect the 1978 anchovy year class. Results of otolith birthdate analysis of recruits from the 1978 year class by Methot (quoted in Lasker, in press) bear this out; recruits were born mainly in March and April 1978, despite extensive spawning in December 1977 through February 1978.

Walsh et al. (1980) also provide evidence from Peru that confirms the idea that strong winds and turbulent seas can be detrimental to the survival of the Peruvian anchovy. On the other hand, Ware et al. (in press) suggest that aggregations of food for Peruvian anchovy larvae may be a *result* of strong winds by the production of Langmuir cells and consequent accumulation of likely food items in "windrows." The space and time scales of the events being considered differ greatly, and reconciliation of these ideas requires additional research into the effects of wind-mixing and the distribution of larval fish food particles.

The findings that anchovy larvae cannot feed on filamentous diatoms (Lasker, 1975, 1978), that only certain food organisms of the right size for feeding are nutritious (Lasker et al., 1970; Scura and Jerde, 1977), and that there is a low probability of the larva encountering copepod nauplii at first feeding (Lasker and Zweifel, 1978) have provided the biological framework with which to predict the quality of the ocean environment for survival of early anchovy larvae. Similar data are needed for other pelagic fish larvae, and studies have begun on a number of commercially important species to test the ideas suggested here (Ellertsen et al., in press).

Predation on Larval Fishes: An Unknown Factor

Predators on marine fish larvae usually are not discussed very much in relation to recruitment, despite the possibility that they may have great effects on larval survival and year class formation. Studies in the laboratory and in the sea have been more qualitative than quantitative. Exceptions to this rule are the recent studies of Hunter and Kimbrell (1980), who demonstrated that anchovy adults can be voracious predators on their own eggs and larvae, and the work of Lillelund and Lasker (1971), who pointed to the possibility that many pelagic copepods co-existing with fish larvae can bite and lethally damage them. Theilacker and Lasker (1974) also implicated euphausiids as potential predators of larval anchovies. Some fish larvae, such as those of the Pacific mackerel, are piscivorous and, in the laboratory at least, are known to eat their siblings (Hunter, this volume). Alvariño (1980), in an interesting investigation of the distribution of larvae, interpreted the inverse relation of patches of potential predators to patches of anchovy eggs and larvae as an evolutionary development in spawning behavior favoring survival of larvae.

Most of the information concerning predation on larval fishes is too sparse and unquantifiable. A great deal of work needs to be done in this area of study and requires a combination of laboratory and field observations before we will be able to assess the role of predation in recruitment processes.

Conclusion

While the bulk of the recruitment research described here has been on clupeoid fishes, the concepts advanced may be applicable to a wide variety of fishes having planktonic larvae. Minimum concentrations of food must be present in the larva's environment with associated stable ocean conditions to insure that threshold-for-feeding concentrations are maintained. Cube-of-the-wind-speed, upwelling, and wind curl indexes are new tools which can be used by fishery scientists to correlate with larval mortality, larval food distributions, and subsequent year-class strength. Biological information on larval fishes obtained in the laboratory now has even greater meaning since it can be used to erect useful predictive models of recruitment and, with specific data on the ocean environment, provides a hope for meaningful fishery prediction. If managers want to respond before there are sudden collapses or substantial increases in fish populations, it seems clear that they must take into consideration the increasing evidence that environmental factors have major effects on the survival of larval fish and that density-independent factors may be more important than previously believed.

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REMOTE SENSING OF ENVIRONMENT 11:439–453 (1981)

The Use Of Satellite Infrared Imagery for Describing Ocean Processes in Relation to Spawning of the Northern Anchovy (*Engraulis mordax*)

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Using satellite infrared thermal imagery in conjunction with extensive sampling for anchovy eggs and adults during March and April 1980, we were able to confirm that large areas of the coastal ocean off California were avoided by anchovies during the peak of spawning due to entrainment into the California Current of ≤14° C water that upwelled north of Point Conception. Upwelling began coincident with the onset of winds from the north and proceeded in pulses separated by a few days. Plumes of upwelled water appeared to be advected southward in ladder-like rows by the California Current. A saline 50+-m-deep warm water pool, 40 km off Ensenada, Baja California, Mexico also was avoided by anchovies. The appearance of an inshore 16° C refuge and an extensive 220-km warm-water "wake" associated with Santa Catalina Island also were observed. Each of these oceanographic features was confirmed by ship observations.

Introduction

The recent acquisition of a satellite remote sensing facility at the Scripps Institution of Oceanography has permitted us to examine thermal imagery of the Pacific Ocean adjacent to the United States–Mexico west coast on a daily basis using the NOAA-6 polar orbiting satellite coincident with fine-grid oceanographic ship observations. Our objectives were to relate variations in mesoscale (approximately 200 km) sea surface temperature distributions with anchovy spawning and to identify and delineate important ocean processes that might be important to the survival of fish eggs and larvae, e.g., upwelling (Lasker, 1978) and offshore transport (Parrish and MacCall, 1978).

During the period of the observations reported here, 14 March to 14 April 1980, a variety of dynamic oceanographic events were observed, including (1) the development of coastal upwelling plumes off Pt. Conception and Pt. Sur, California; (2) the entrainment of these cold-water plumes into the southward-flowing California Current; (3) the formation of an extensive "wake" associated with Santa Catalina Island; (4) the development of a

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warm-water refuge in the Southern California Bight between Santa Catalina and the coast; and (5) the formation of sharp oceanic frontal boundaries. These are described in the following sections and discussed in relation to anchovy spawning, egg, and larva distribution, and larval survival.

Surveys are made each spring of recent anchovy spawning in order to estimate anchovy spawning biomass and include sampling of anchovy eggs, larvae, and adults as well as physical oceanographic measurements. During the spring of 1980, clear skies prevailed during the observational cruise of the R/V *David Starr Jordan*. Satellite infrared images were collected concurrently with ship observations.

Methods

Remote sensing

The Scripps Institution of Oceanography Remote Sensing Facility has a direct reception antenna and terminal, an information handling subsystem and an interactive digital image manipulation system. The facility can receive the analog AVHRR data directly from the NOAA-6 polar orbiting satellite and convert it to digital form. The data are then analyzed on a video display or stored on computer magnetic tape for further processing and analysis. Images for this study were collected from 14 March 1980 through 14 April 1980. The area studied extended from approximately Monterey Bay, California (37°N, 122°W) to Vizcaino Bay, Baja California, Mexico (28°N, 115°W) and out to sea about 400 n. mi. from shore. Within this region, particular attention was directed to the Southern California Bight area, approximately 32°N to 34°30′N and 117°W 121°W. NOAA-6 satellite passes were collected daily or twice a day. For daytime passes, clouds and atmospheric effects were seen using the NOAA-6 visible channel. For nighttime passes, clouds and atmospheric effects were evaluated on the basis of the time persistence of ocean features compared to the more rapidly changing atmosphere. The infrared data were enhanced to cover the full range of sea surface temperature sensed by the radiometer. Temperature calibration of each image was done by relating pixel gray-scale values to same-day sea surface temperature observations from ships at several locations. Computer programs for processing and analyzing the data were made available to us by the staff of the Scripps Remote Sensing Facility.

Shipboard observations

The National Oceanic and Atmospheric Administration research vessel *David Starr Jordan* recorded discrete surface temperatures at all stations with a bucket thermometer; salinities and temperature were continually monitored also with a thermosalinograph throughout the sampling area from San Francisco to central Baja California, out to approximately 200 n. mi. Oceanographic and biological sampling stations were occupied along the normal California Cooperative Oceanic Fisheries Investigations survey (CalCOFI) lines (Kramer et al., 1972) and at more closely spaced intervals in selected areas.

A vertical plankton tow of 1-min duration was taken from 70-m deep with a 0.333-mm mesh conical net of 25-cm diameter every 4 n. mi. along the grid to collect anchovy eggs (Stauffer and Picquelle, 1980). Nine-hundred and sixtyone stations were sampled in water ranging from 11° to 17.5° C. Fifty-two hauls were taken with a midwater trawl to sample for adult anchovies in the upper mixed layer. The temperature relationship between spawning and temperature was investigated further by examining records of five March–April CalCOFI cruises from 1969 to 1979 for anchovy egg occurrence versus temperature.

Evaluation of the Northern California coastal upwelling plumes

The changing areal extent and southward progression of cold-water upwelled plumes were examined in a series of infrared images collected during the period of this investigation. Two images recorded nine days apart (19 March and 28 March) for the southern California Bight reproduced in Fig. 1, (a) and (b) respectively, illustrate the evolution of coastal upwelling plumes originating off Point Conception in late March 1980.

For the purpose of this study, the differences in gray tone are taken as indications of sea surface temperature changes. An increase in the extent and intensity of light tones relates to a decrease in sea surface temperature. Clearly evident are the upwelling pulses which developed north of Pt. Conception and which appear to become entrained as they intrude into the southward-moving California Current. One interpretation is that once formed each plume advanced southward carried by the California Current and retained its basic shape in ladder-like sequence (see also Fig. 4). Eventually these plumes of cold water merge and assume a southward-pointing tongue that does not significantly invade the Southern California Bight inshore of about 150 km. This large cold-water incursion with a leading edge of 14.5–15.0° C was confirmed by shipboard surface temperatures, 27 March to 12 April (Fig. 2). Sea surface temperature isotherms derived from satellite imagery compare remarkably well with those from shipboard observations as shown at the bottom of Fig. 2. Salinities taken concurrently [see Fig. 3(a) and 3(b)] bore out the conclusion that cold water was upwelled near Pt. Conception and Pt. Sur since salinities inshore were high and isohalines were crowded around shoreline centers of cold water, a characteristic of upwelling (Reid et al., 1958).

Anchovy spawning in the Southern California Bight and cold-water intrusion from Northern California upwelling centers

Despite the "snapshot" nature of 6 April infrared imagery (Fig. 2) of the Southern California Bight, previous and subsequent photographs show clearly that the mesoscale features of surface temperature change slowly so that, for a given day, the temperature distribution does not appear to be markedly different from the preceding or following day. The slow-changing behavior of mesoscale thermal features off California was first described by Bernstein et al. (1977). Thus the biological sampling done over a few days can be compared to a single day's infrared image.

In this study, because thermal imagery was taken coincident with anchovy egg and adult sampling, it was possible to compare sea surface temperature with spawning incidence. Figure 4 is a thermal image from 6 April which has superimposed on it the geographic distribution of anchovy egg catch. The distribution of first-day anchovy eggs clearly showed that nearly all spawning was confined to the

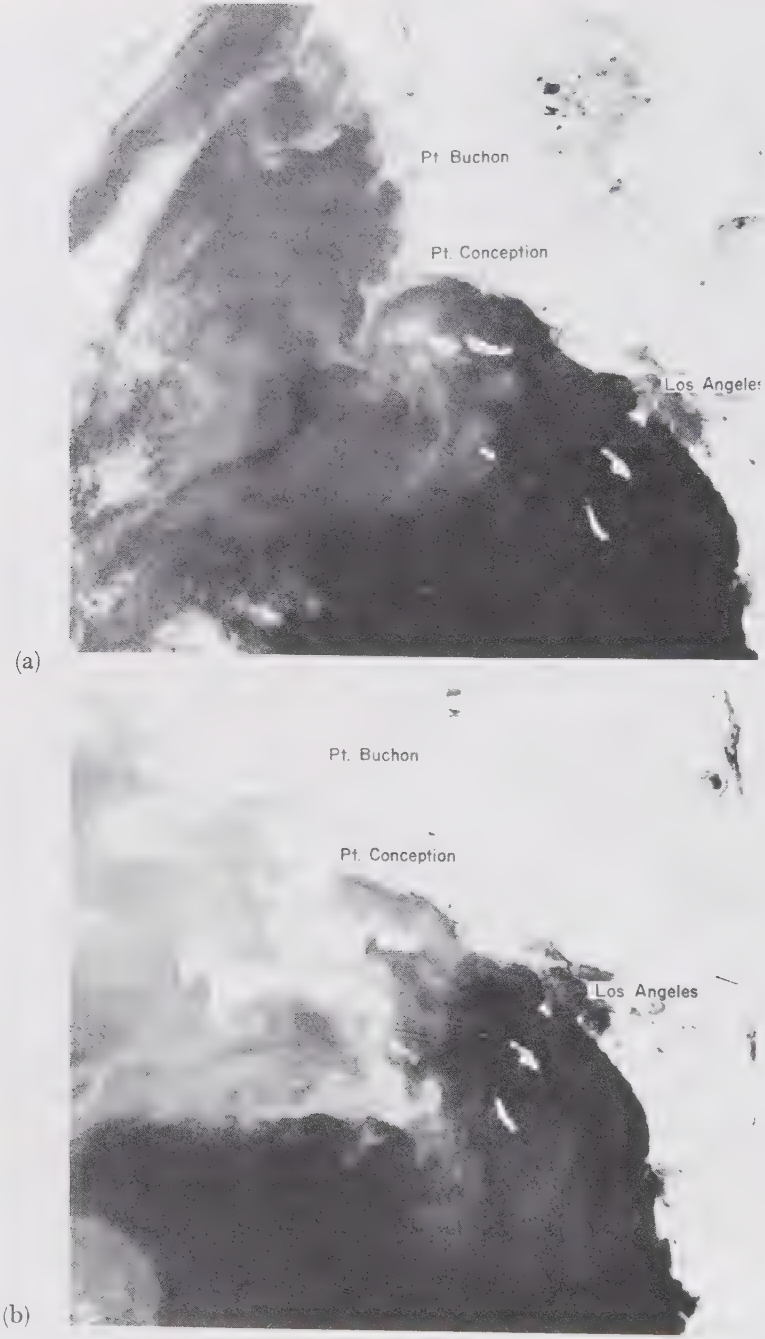


FIGURE 1. NOAA-6 infrared photographs from Pt. Sur, California to Ensenada, Baja California. (a) Upwelling began along the northern California coast about 14 March 1980 and was well established on 19 March when this photo was taken. (b) Nine days later cold water from upwelling was extensive and additional upwelling plumes established at and north of Pt. Conception. Warm-water wakes are seen from virtually all the islands in the Southern California Bight.

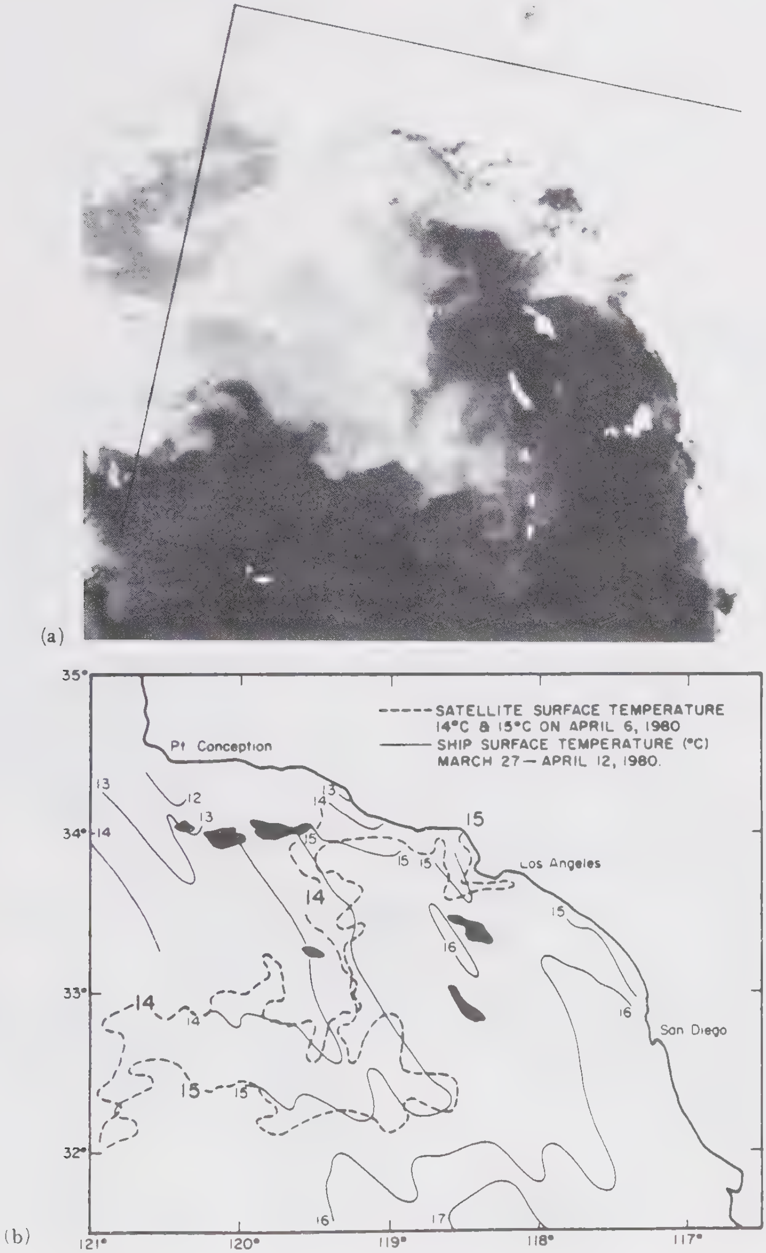

(a)
(b)
35°
34°
33°
32°
121°
120°
119°
118°
117°
SATELLITE SURFACE TEMPERATURE 14°C & 15°C ON APRIL 6, 1980
SHIP SURFACE TEMPERATURE (°C) MARCH 27 — APRIL 12, 1980.
Pt Conception
Los Angeles
San Diego
12
13
13
13
14
14
14
14
15
15
15
15
15
15
15
16
16
16
17

FIGURE 2. Match of satellite and ship sea surface temperatures. (a) 6 April 1980 NOAA-6 infrared photograph showing cold water extending south. (b) Match of 27 March to 12 April ship surface temperature observations with contoured gray-scale-derived temperatures (6 April 1980).

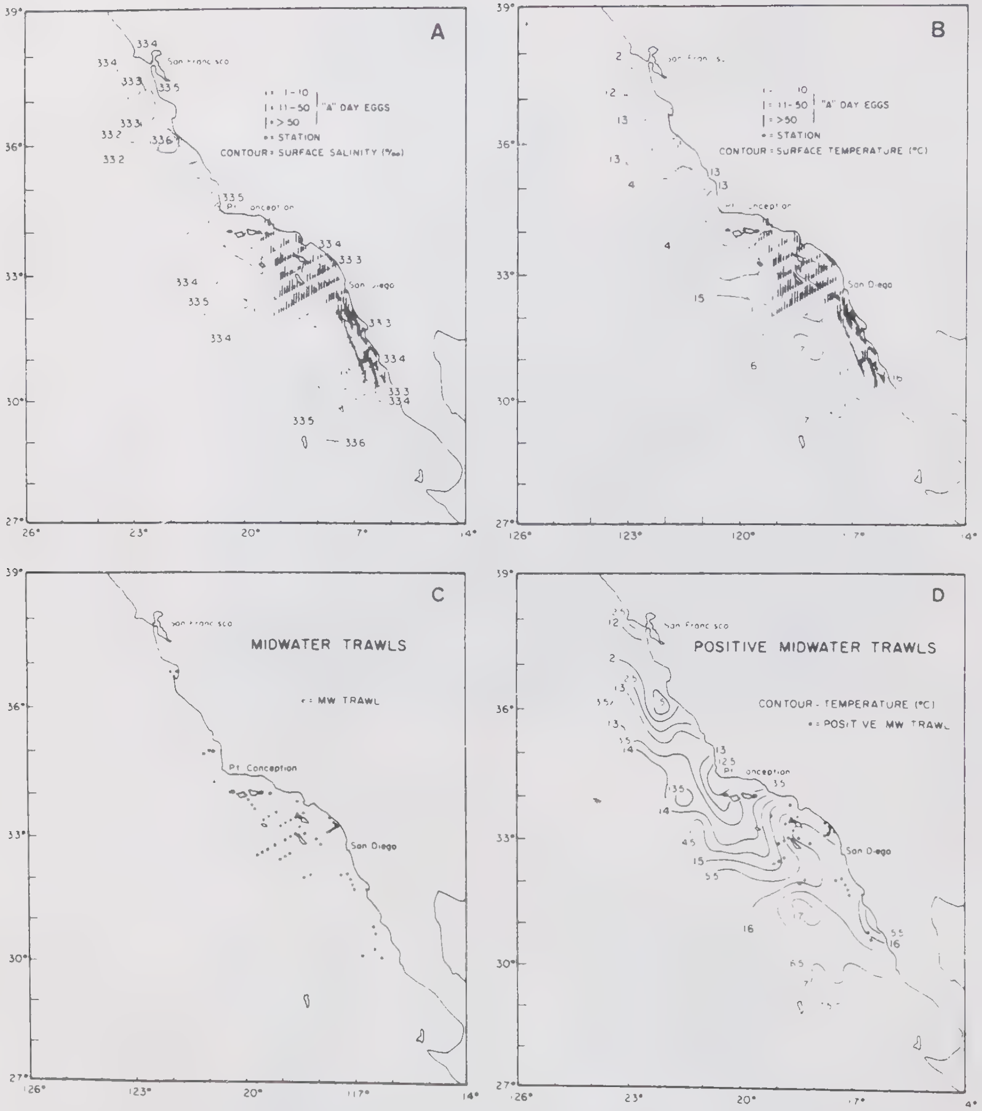


FIGURE 3. Distribution of anchovy eggs and adults in relation to salinity and temperature. (a) First day of spawning eggs and salinity. (b) First day of spawning eggs and surface temperature. (c) All midwater trawls taken from 27 March to 12 April 1980 by R/V *David Starr Jordan*. (d) Adult anchovy catches by midwater trawls and temperature distribution. Compare this with Figure 4(b).

Southern California Bight [Figs. 3(b) and 4]. The seaward extent of spawning was apparently abridged by the southward intrusion of recently upwelled water indicated by the 14° C isotherm. The series of infrared images examined showed that a large pool of warm water which had been prevalent prior to upwelling, was displaced by this southward flow. Thus during late March and early April 1980 there were two distinct temperature regimes in the general geographic region where anchovy spawning normally takes place. There was a cold area resulting from upwelling off Pt. Conception and north and a large warm area which extended from Baja California into the Southern California Bight and approximately 185 km offshore. An infrared image from 28 March of the California

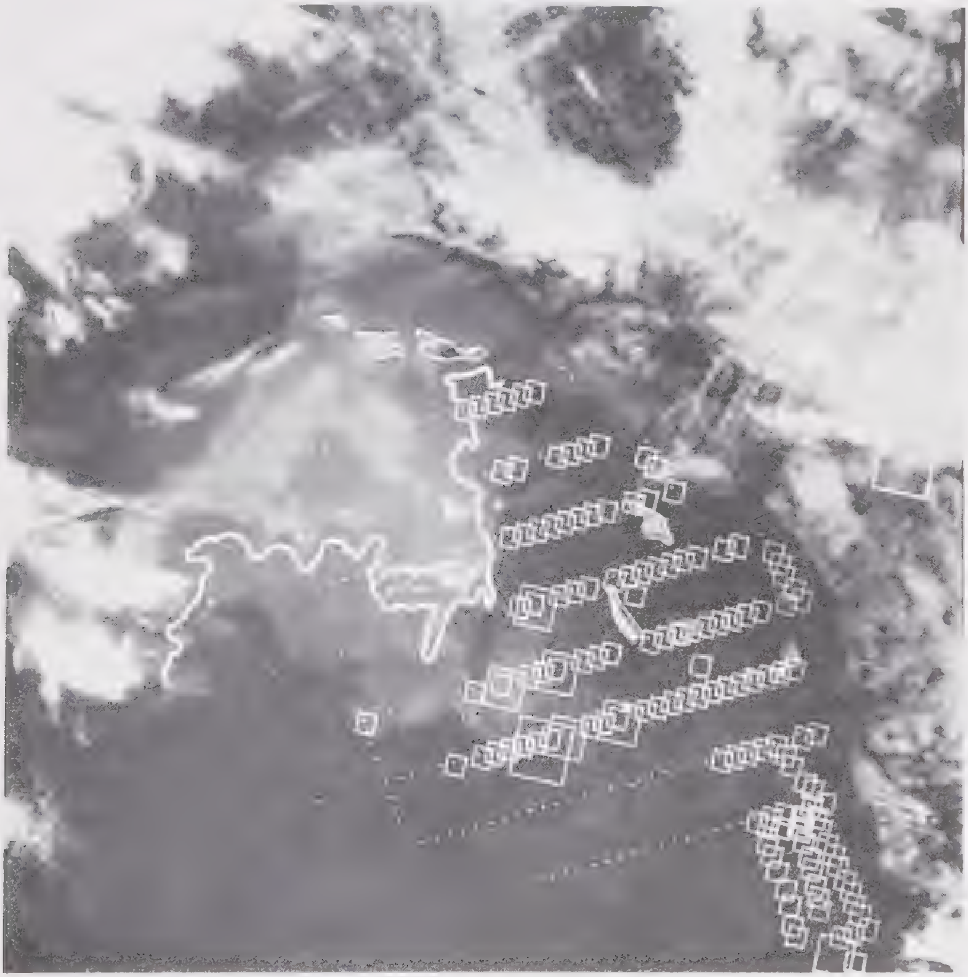
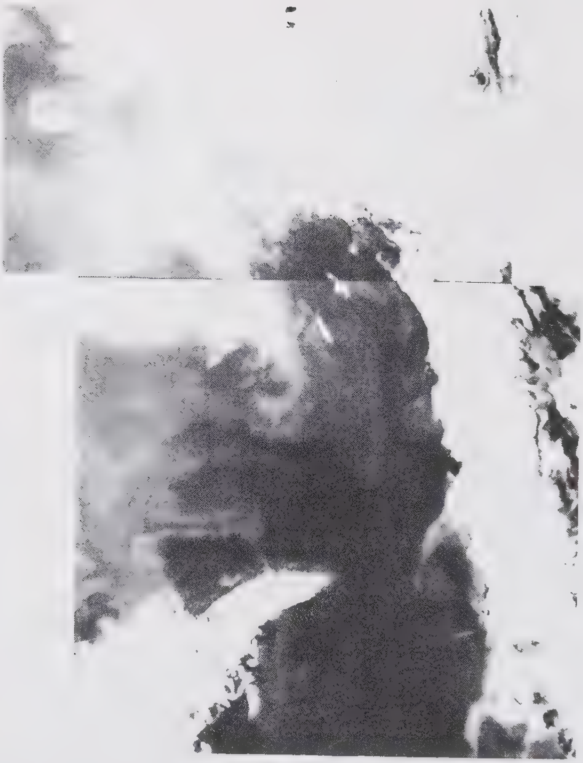


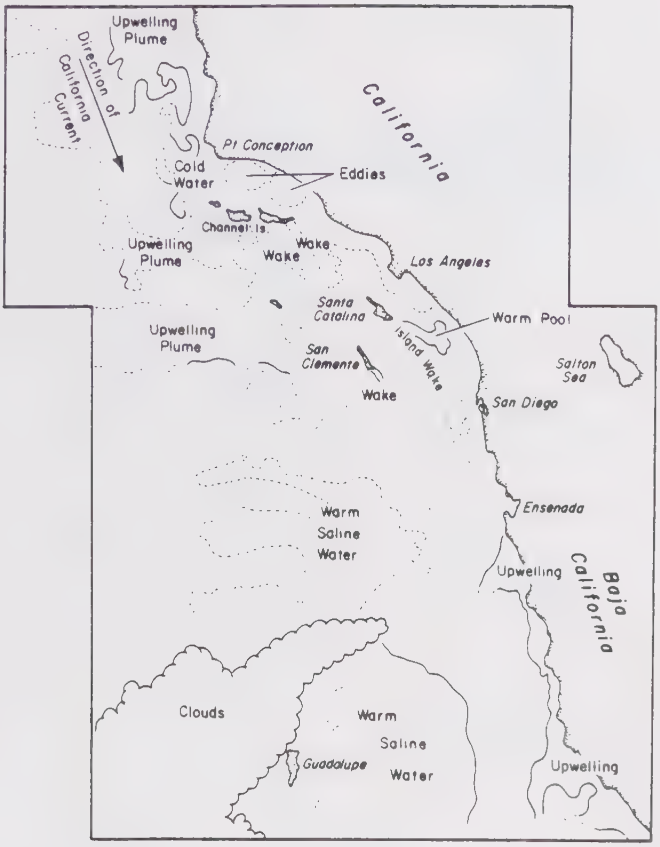
FIGURE 4. Distribution of anchovy eggs superimposed on the thermal image of the Southern California Bight taken 6 April, 1980. The 14° C isotherm plotted from satellite gray-scale calibration has been drawn in. Feathery white objects are clouds. Squares indicate number of anchovy eggs under one square meter of sea surface.



(a)

FIGURE 5. Infrared photograph from NOAA-6 showing California Current and Southern California Bight region, 28 March 1980. Note the sequential westward upwelling plumes descending from Pt. Conception. The large warm (17° C) saline (33.5–33.6‰) pool west of Ensenada and east of Guadalupe Island was an effective barrier to anchovies. The Southern California Bight had a temperature regime intermediate (14.5–16° C) to the upwelled water moving south outside the Channel Islands and the warm saline pool off Baja California.

Current and the coast of California and Baja California, shown in Fig. 5(a), illustrates the features just described. In Fig. 5(b) is our interpretation of the image. The satellite temperature/anchovy egg findings are corroborated by mapping the distribution of first day eggs on sea surface temperature observations made concurrently aboard ship. The histograms in Fig. 6 show that anchovy did not enter water colder than 12.5° C nor warmer than 17° C in March–April 1980. However, most of the stations where eggs were found were in water warmer than 14° C. This was unexpected since 14° C is the normal spawning temperature for the northern anchovy. Data from March–April 1969, 1972, 1975, 1978, and 1979 CalCOFI cruises are also shown in Fig. 6 (a). In earlier years appreciable spawning took place at temperatures above 16.5° C and in water colder than 14° C. The



(b)

FIGURE 5. continued.

modal temperature for anchovy spawning in March and April from 1969 to 1979 was 14–15° C, but was 15–17° C in March–April 1980.

In 1980, the determination of the age of each egg provided additional information on the drift of anchovy eggs and the integrity of the water masses in which they were spawned.[1] Figure 6 shows that each of 3 days' concurrent spawning throughout the spawning range of the anchovy were remarkably similar in temperature distribution. Our conclusion from this comparison is that transport or drift was not extensive for at least 3 days after spawning and that anchovy eggs stay with the water mass in which they are spawned. Thus despite the gradual day-to-day southward progression of the cold wedge of previously upwelled water by the California Current observed by satellite, warmer water outside the wedge remained intact. Thus eggs and larvae in warmer water were not subjected to colder temperatures since advective mixing was minimal judging from the satellite photographs. In fact, in the middle of this month-long period of satellite radiometer

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[1] Eggs were not staged as they were in 1980, thus 3 days of spawning are represented in the composite histogram of mean values (Fig. 6).

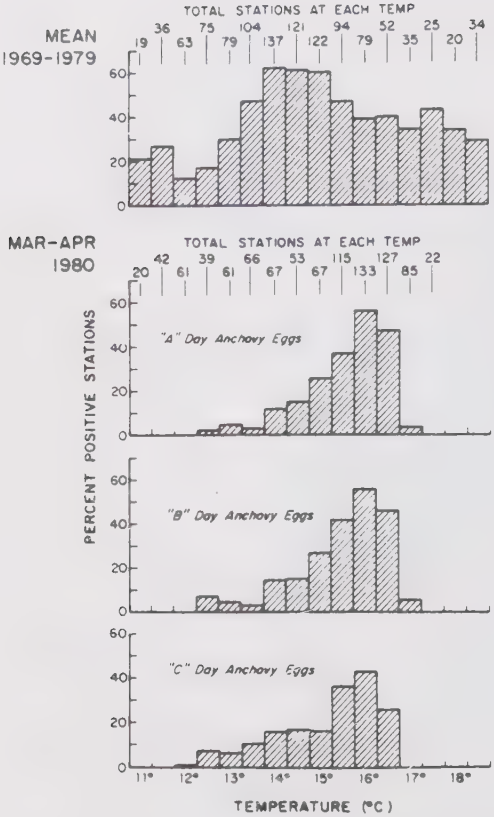

FIGURE 6. Percent of stations at different temperatures where anchovy eggs were found during March and April, the peak of the anchovy spawning season. (a) Average of 5 cruises (1969, 1972, 1975, 1978, and 1979). Note that modal temperature is 14–15° C; eggs were not staged. (b) Percentage of stations with anchovy eggs in 1980. A, day eggs are less than 24 hr old; B, eggs are between 24–48 hr old; C, eggs are from 48–72 hr old. Modal temperature in 1980 was 16° C.

observations, a storm swept through the area on 1 and 2 April, while ship sampling continued. Except for blurring of frontal temperature gradients, no major change in the surface thermal features could be seen.

Indicators of larval drift and exclusion of adults by upwelling

Relatively high numbers of anchovy larvae were found in plankton hauls taken by the Russian vessel, R/V *Tikhookeanskiy*, in the coastal area north of Pt. Conception in February 1980. Temperatures were very warm for this entire zone in February; for example, 10-m temperatures off San Francisco were 13°–14° C, compared to 11–12° C found normally, with progressively warmer conditions to the south, i.e., 15° C for the line of stations off Pt. Conception. Winds were light and from the south prior to March 11 and upwelling was minimal, judging from average wind speed at Pt. Conception (Fig. 7). Winds from the north increased markedly on March 12 and persisted. When the area north of Pt. Conception where anchovy larvae had been collected in February, was sampled in March, no larvae of any age were found. This suggests that the extensive upwelling as indicated by wind data and observed by satellite carried anchovy larvae out of the coastal zone and into the California Current while at the same time adult anchovies were excluded as evidenced by lack of fish in trawls [Fig. 3(c) and (d)]. The start of upwelling on 14 March and the progressively colder temperatures appeared to have excluded anchovies from that time on. The leading edge of the cold-water mass generated 14 March by upwelling off Pt. Conception by 6 April travelled south approximately 300 km at a rate of about 12.5 km/day.

Exclusion of anchovies from a warm saline zone off Baja California

Satellite pictures (Fig. 5) reveal the large areal extent of a warm region of 17° C and warmer off Ensenada, Baja California. In previous years 17° C has been compatible with spawning (Fig. 6), but spawning in 1980, however, was restricted to a band 40-km wide, parallel to the Baja California coast avoiding this

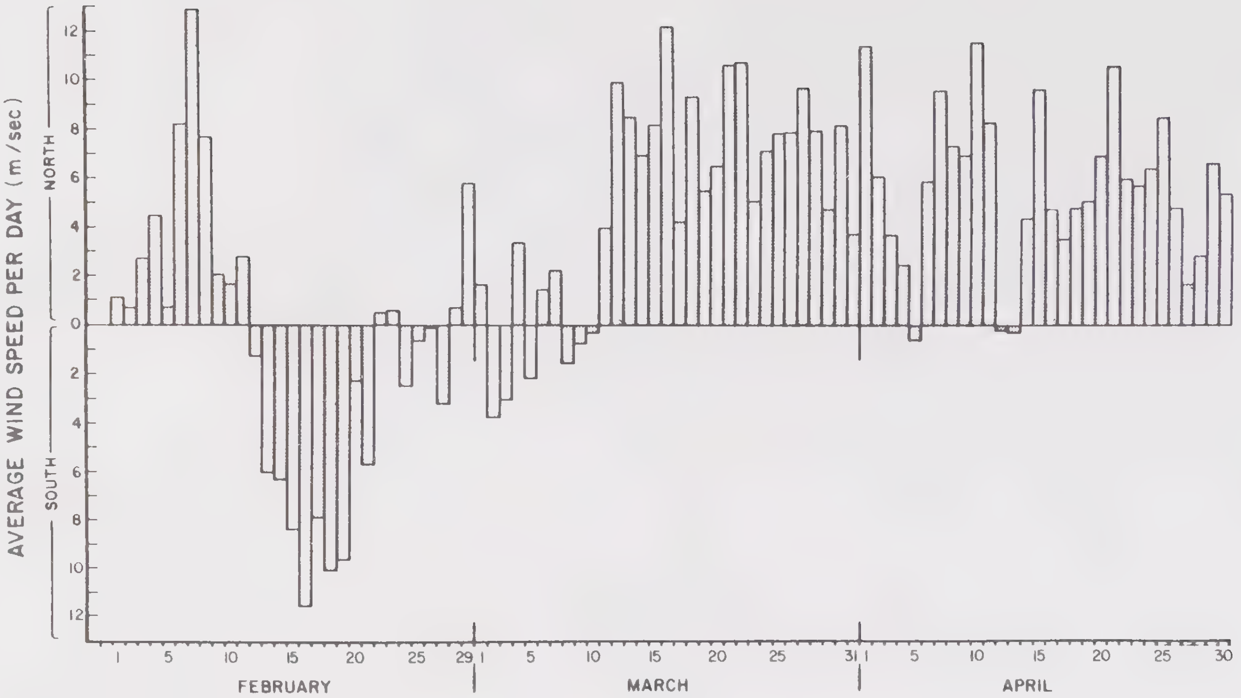

FIGURE 7. Average windspeed per day at Pt. Conception, California, February–April 1980. Upwelling was first observed by satellite at Pt. Conception on 14 March (see Fig. 2) and after sustained southward winds began. North = winds from the north; South = winds from the south.

warm pool. Higher salinities were coincident with this warmer water [Fig. 3(a)]. Anchovy spawning was restricted to the east of this warm water pool [Fig. 3(b)]. Upwelling centers along the Baja California coast brought up 15°–15.5° C water but did not exclude anchovy spawning [Fig. 3(b)]. Earlier surveys of anchovy larvae distribution show that in most years this geographic area northeast of Guadalupe Island is usually devoid of anchovies (Kramer and Ahlstrom, 1968) but no analysis of oceanographic features has yet been made to confirm whether warm saline water is the reason for this in every case.

Ocean upper mixed layer characteristics

Expendable bathythermographs were deployed along some of the March–April anchovy sampling lines to determine the depth of the mixed layer. Throughout the survey area, the mixed layer was about 50-m deep or deeper. Thus the surface temperatures, as recorded by satellite, accurately reflected definable upper layer water masses and their movements. Upwelling areas similarly were distinct. An examination of Fig. 8 shows that CalCOFI Line 100, off Ensenada, on March 26–27 was characterized by the 60-m deep high-salinity 17° C pool which anchovy avoided during spawning. CalCOFI Line 90, off San Onofre, California, showed contrasting temperature regimes, the coastal warm band (15°–16° C), and the intrusion of colder (ca. 14° C) water from the north, confirmed by the satellite photo of 6 April shown in Fig. 2. Vertical temperature sections on CalCOFI Line 80, off Pt. Conception, were taken later in April (20 April) but still show the characteristic upslope of the 11° and 12° C isotherms typical of an upwelling regime.

Island Influences

The Channel Islands of Santa Cruz, Santa Rosa, and San Miguel, appear to isolate portions of the Southern California Bight (Pirie and Steller 1977), from the influx of the cold water upwelled from Point Conception (Fig. 5, 28 March 1980).

Circulation in the Southern California Bight seems to be influenced by Santa Catalina Island, as shown in the satellite picture in Fig. 5. Cool water streaming from the north is shielded from the inshore zone by the island. A warm-water "wake" is apparent in the 28 and 29 March infrared photographs extending 225 km between two colder water masses and persisting for at least 5 days afterwards. Upwelling does not define the shoreward edge of the wake since no upward-sloping isotherms were seen in vertical sections. The R/V *David Starr Jordan* fortuitously crossed this wake on 30 March 1980 while recording sea surface temperature with a thermosalinograph and bucket thermometer. This is shown in Fig. 9, confirming the usefulness of the satellite infrared photograph. This unusual oceanographic feature would have been undetected and its dimensions unrealized from sea surface measurements alone.

Discussion

Because satellites can see vast areas of the ocean day in and day out, they provide the scientist with a synoptic look at processes only seen heretofore on smaller scales and restricted to the times when a ship or ships can cover the area of interest. In this study, only a satellite could have provided us with a synoptic picture of the large scale oceanographic events which were happening over the entire

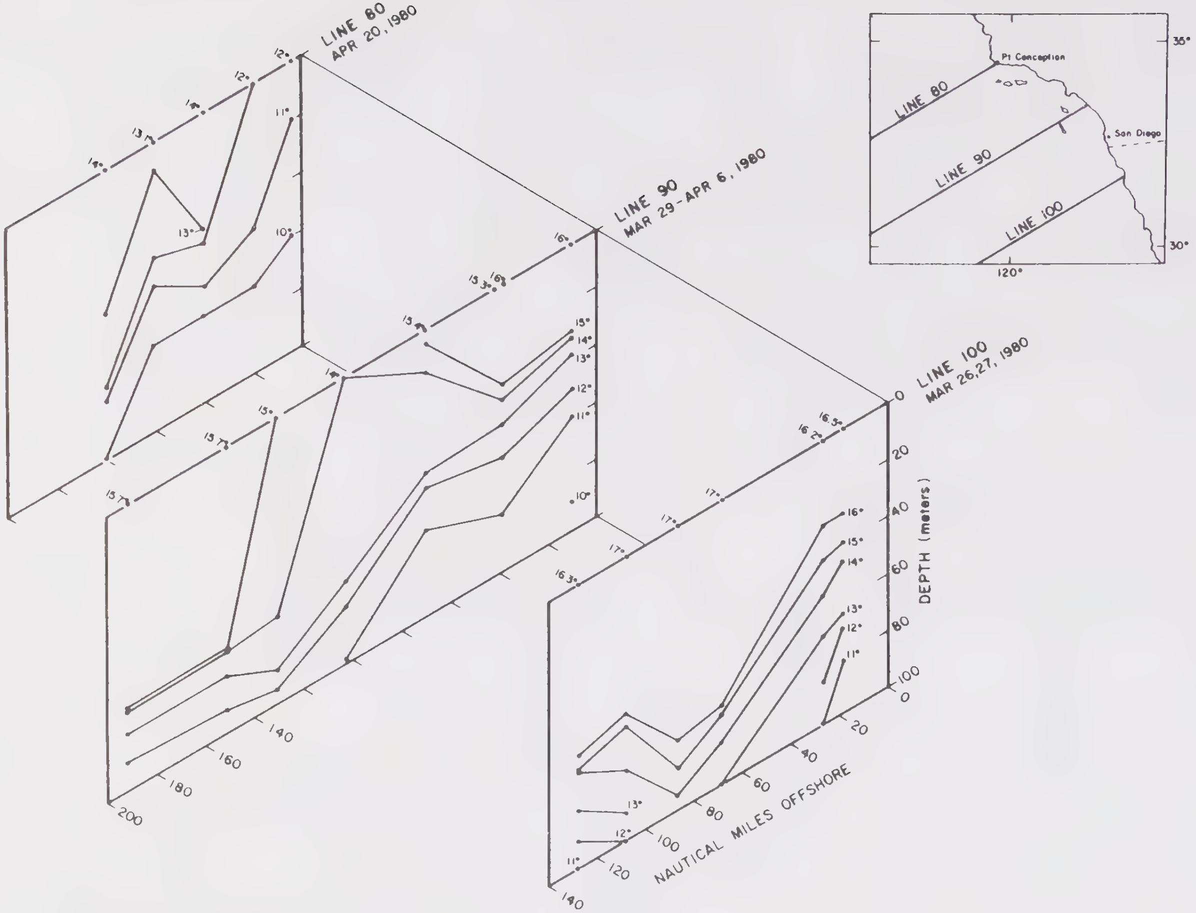

FIGURE 8 Temperature cross sections taken by the R/V *David Starr Jordan* with expendable bathythermographs across the California Current and the Southern California Bight. Line 100, off Ensenada, Baja California, shows that the warm saline pool identified by satellite and surface measurements was about 70-m deep at its deepest point. Line 90, off San Onofre, California showed the southerly extent of a core of cold, upwelled water. Line 80 had 11 and 12° C isotherms sloping up and nearshore, characteristic of an upwelling regime.

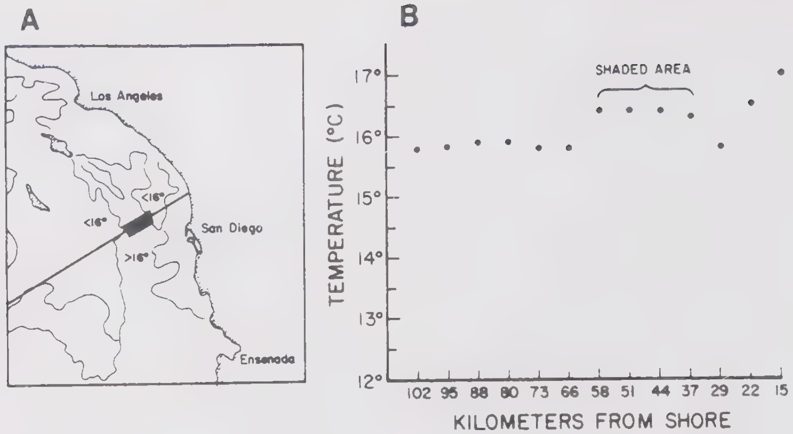

FIGURE 9. Satellite and ship identification of a remarkable wake extending from Santa Catalina Island, 28 March 1980. (a) ship track and temperature contours drawn from satellite photograph shown in Fig. 5. (b) sea surface temperatures recorded by bucket thermometer on the same day.

spawning area of the anchovy during the peak of the spawning season. The extensive ground truth provided by the R/V *David Starr Jordan* confirmed that the 0.5° C accuracy of the infrared radiometer aboard most of the NOAA satellites accurately detects the movement of surface layers and shows the sequential development of upwelling along the California coast over large areas of ocean. The tight correlation between temperature and anchovy spawning was unexpected; when other variables (e.g., salinity) are considered, we are led to the conclusion that temperature is not the environmental variable responsible for anchovy distribution in March–April 1980. Rather, temperature can be used as an indicator of water masses. Sette (1960) in describing ship observations he made in 1940, said, "there was a cold tongue extending down from Pt. Conception into our (sardine) spawning area… the spawning tended to be concentrated around the periphery of this cold tongue." He went on to state that he believed the spring bloom of phytoplankton–zooplankton probably occurred at the leading edge of this cold water and that this may have been the reason for sardine spawning there.

Thus, sardines and anchovies respond similarly and some general principles of animal–environment interaction may be responsible for pelagic fish spawning distribution. Satellites permit us to view synoptically vast areas not possible with a ship alone. With sensors for wind, chlorophyll, and wave height, a suite of information may make it possible to use ships more effectively for the study of fish egg and larval distribution and mortality, particularly by judicious deployment of ships guided daily by satellite information. Such information is vital for effective management of certain marine fishery resources.

We are grateful to Margaret Wolfe who assisted us in our early work at the Scripps Remote Sensing Facility. Thanks also to Richard Charter for development of computer routines which simplified our use of

R/V David Starr Jordan *and other CalCOFI data and to Andrew Bakun who provided the geostrophic wind data. Gary Stauffer was Chief Scientist on the R/V* David Starr Jordan *during the collections of anchovies and their eggs.*

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GROWTH RATES OF NORTH PACIFIC ALBACORE, *THUNNUS ALALUNGA*, BASED ON TAG RETURNS

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ABSTRACT

Estimates of growth parameters for North Pacific albacore, *Thunnus alalunga*, were based on tag-recapture statistics, using the standard von Bertalanffy model and an extended model. Sequential estimation of L_∞ and K allowed us to test hypotheses concerning variation in growth rate between tagged albacore recaptured in different ocean regions.

Significantly lower growth rates were found in albacore recaptured off Japan and the United States north of latitude 40° north compared with those recaptured off the United States south of latitude 40° north. The differences in estimated growth rate were generally consistent with differences in length-frequency distributions of albacore taken off the United States north and south of latitude 38° north during the period when most recaptures were made. The findings add to a growing body of evidence that the North Pacific albacore population is not homogeneous; rather, at least two different subpopulations may exist.

Growth rates of North Pacific albacore, *Thunnus alalunga* (Bonnaterre), have been estimated by counting vertebral rings (Uno 1936; Aikawa and Kato 1938; Partlo 1955), examining scale circuli (Nose et al. 1957; Bell 1962; Yabuta and Yukinawa 1963), tracing progressions of length modes (Brock 1943; Suda 1954), and by measuring tagged fish at release and recapture (Otsu 1960; Clemens 1961). Of these techniques, only tagging provides direct estimates of growth rate, and the tagging results of Otsu and Clemens are reasonably consistent with the conclusions of Yabuta and Yukinawa's scale analysis and Suda's modal progression work. However, as Shomura (1966) noted in a review of tuna growth studies, comparisons are complicated by the biases and uncertainties peculiar to each method. For example, in the case of tagging we assume that the growth rate is unaffected by stresses resulting from capture, handling and tagging, and from the burden of carrying the tag itself. Conclusive results will require that the basic assumptions of any particular method be tested and verified.

In this paper, we present new estimates of growth parameters based on recent tag-recapture experiments conducted jointly by the National Marine Fisheries Service (NMFS) and the American Fishermen's Research Foundation (AFRF).[3] We use the standard von Bertalanffy growth model, but also briefly explore an extension. Sequential estimation of the parameters L_∞ and K allows us to test hypotheses concerning variation in growth rate between tagged fish recaptured in different ocean regions.

Transpacific recaptures of albacore tagged in the eastern North Pacific off North America and in the western North Pacific off Japan have established the interdependence of the United States and Japanese North Pacific albacore fisheries, and have also fostered the hypothesis of a single, common stock (Ganssle and Clemens 1953; Clemens 1961; Otsu and Uchida 1963). However, our results add to growing evidence (Laurs and Lynn 1977) that the North Pacific albacore population is not homogeneous, as usually assumed, but is composed of at least two subgroups with different migration patterns and growth histories.

METHODS

Tagging Procedures

Albacore were caught in the eastern North Pacific and tagged aboard U.S. commercial jig and

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[3] AFRF administers revenues derived from a landing assessment paid by the U.S. albacore industry on U.S.-caught albacore.

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bait fishing vessels on charter to AFRF. Approximately 70% of the tagging was done by commercial fishermen trained in tagging procedures, the rest by NMFS technicians. Single Floy[4] spaghetti-dart tags were inserted on the left side below the second dorsal fin with the aid of a beveled stainless steel tube so that the tag barb was lodged in the pterygiophores of the fin. Only fish judged to be in very good condition were tagged; fish hooked in the roof of the mouth or showing signs of extreme exhaustion or severe bleeding were rejected. For each tagged fish a record was kept on 1) tag number, 2) date and time of release, 3) fork length at time of release, 4) condition at tagging, and 5) longitude and latitude of release. Additional tagging details are given in Laurs et al. (1976).

Recovery Procedures

Recoveries were made by sport and commercial fishermen, unloaders, and cannery workers. Information was obtained on 1) tag number, 2) date of recapture, 3) fork length at time of recovery, and 4) longitude and latitude of recapture. Most recapture locations were given as loran coordinates, which were converted to longitude and latitude, but the recapture locations for tags recovered by unloaders and cannery workers were often reported inexactly, e.g., as "off central California." Direct measurements of fork length were available for about one-half the fish recovered. For most of the remainder only the weight at recovery was given, and fork length was estimated using Clemens' (1961) weight-length relation. Observed fork lengths were measured to the nearest centimeter. Bias in estimating fork length from observed weight using the inverted weight-length relationship was judged to be <0.5 cm in absolute value over the length range represented in the recapture sample, so subsequent growth analyses were based on the combined sets of observed and estimated lengths.

Data Screening

The tag return data were screened to exclude cases where information was incomplete, unreliable, or clearly inaccurate. Out of 741 tag returns made from 1971 through 1978, 305 were rejected (Table 1). In 15 cases length at release was not measured, in 116 cases the recapture date was unknown, and in 68 cases neither length nor weight was measured at recovery. In 79 other rejected cases the length at recovery was not measured and the weight only guessed without the use of scales. Additionally, in 27 instances a gross error was apparent in the measurement of fork length either at release or recovery.

The final accepted data set of 436 cases includes observations on 28 albacore showing negative estimated growth. We assume these are a result solely of measurement error or error in estimation in cases where the recovery weight was converted to length, and we assume such error occurs throughout the data set independently of size or time between release and recapture (time out).

One of the common steps in screening tag recovery data for growth studies is to partition the data according to length at release, compute linear regressions of growth increment on time out within each subset, and then reject rare observations, usually those departing from expectations by more than two standard deviations (Schaefer et al. 1961; Joseph and Calkins 1969). We abandoned this step because the number of

TABLE 1.—Summary of number of tagged fish released, recovered, rejected, and accepted for analysis of albacore growth.

			Rejected tag recoveries (no.)						
Year	No. tagged fish released	No. tagged fish recovered	Missing release length	Missing recapture date	Missing recovery size	Weight at recovery estimated	Measurement error	Total	No. tag recoveries accepted for analysis
1971	887	34	2	6	5	1	0	14	20
1972	1,557	132	1	23	13	16	10	63	69
1973	1,805	111	0	23	10	12	2	47	64
1974	2,486	175	4	22	16	22	8	72	103
1975	1,349	115	1	17	13	15	2	48	67
1976	1,581	85	0	15	8	10	3	36	49
1977	1,221	25	0	4	0	3	0	7	18
1978	2,719	58	1	6	3	0	2	12	46
Unknown	—	6	6	—	—	—	—	6	0
Total	13,605	741	15	116	68	79	27	305	436

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[4] Mention of a commercial company or product does not constitute an endorsement by the National Marine Fisheries Service, NOAA.

"outliers" it identified was consistent with the number expected due to chance alone, because the procedure has no sensible stopping rule, and because even with length at release fixed, the expected relationship between growth increment and time out is nonlinear.

Grouping of Data

The selected data were cross-classified by location of tagging and location of recapture (Table 2). Nearly 66% of the 436 tagged fish were released inshore,[5] and of these 74% were released south of lat. 40° N, the remainder north of this latitude. Eighty-four percent of recaptured fish released inshore south of lat. 40° N were recovered in the same area, 5% were recovered inshore north of lat. 40° N, 1.4% were taken in the offshore area east of long. 180°, and 8.4% were recovered in the western Pacific. Of the recovered fish tagged and released inshore north of lat. 40° N, only 8.2% were recaptured inshore south of lat. 40° N, 1.4% were taken east of long. 180° in the offshore area, 27.4% were recovered in the area of tagging and 63% were recovered in the western Pacific. Of the recovered fish tagged offshore, 70.5% were recaptured either inshore north of lat. 40° N or west of long. 180°, and only 27.5% were recovered in the southern inshore area.

For purposes of constructing and testing hypotheses about differences in growth rates, tag returns were grouped into three categories depending on recapture location: 1) Group A includes all fish recaptured inshore south of lat. 40° N, except those released inshore north of lat. 40° N (221 fish). 2) Group B consists of tag recoveries made inshore north of lat. 40° N, excluding those released inshore south of lat. 40° N (75 fish). 3) Group C consists of all tag recoveries made west of the 180° meridian (114 fish). The three groups together comprise 410 recaptures. Excluded are 6 fish tagged inshore north of lat. 40° N and recovered south of this line the following year or later; 11 fish released south of lat. 40° N and recaptured in the northern inshore area (1 the same season, 10 in following years); 6 fish recaptured offshore east of long 180°; and 3 fish whose recapture locations are unknown.

Growth Models

We used observations of growth increment, length at tagging, and time at liberty to estimate the growth rate, K, and the asymptotic length, L_∞, of the standard deterministic von Bertalanffy model. In addition, we considered an extension of the von Bertalanffy model which allows the growth rate to vary with age in a simple manner. In general terms, we assumed that the expected growth increment for the jth fish in the ith group ($i = 1,\ldots, m$; $j = 1, 2,\ldots, n_i$), given the initial length and time out, could be stated as

$$E(\Delta L_{ij}) = \int_{t_{ij}}^{t_{ij}+\Delta_{ij}} G(u)\,(L_\infty - L(u))\,du,$$

where $E(\Delta L_{ij})$ = expected growth increment of jth tagged fish in ith group during $(t_{ij}, t_{ij} + \Delta_{ij})$
$= L(t_{ij} + \Delta_{ij}) - L(t_{ij})$
t_{ij} = age of jth fish in ith group at time of release
Δ_{ij} = time at liberty for jth fish in ith group
$L(u)$ = length at age u
L_∞ = asymptotic length
$G(u)$ = unspecified age-dependent growth rate.

If we set $G(u) = K$ = constant, we have the standard von Bertalanffy model, and

$$E(\Delta L_{ij}) = (L_\infty - L_{1_{ij}})\,[1 - \exp(-K\Delta_{ij})],$$

where $L_{1_{ij}} = L(t_{ij})$.

We call this Model 1. (We omit subscripts on

TABLE 2.—Classification of selected tag data by locations of release and recapture.

	Release location				
	Inshore[1]—from lat. 40° N				
Recapture location	South	North	Total	Off-shore	Grand total
East of long. 180°	194	27	221	98	319
Inshore[1]	191	26	217	96	313
South of lat. 40° N	180	6	186	41	227
North of lat. 40° N	11	20	31	55	86
Offshore	3	1	4	2	6
West of long. 180°	18	46	64	50	114
Unknown	2	0	2	1	3
Grand total	214	73	287	149	436

[1] See text footnote 5.

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[5] Fish released (recaptured) east of long. 130° W in the area south of lat. 49° N, or east of long. 135° W between lat. 49° and 54° N were considered to be released (recaptured) inshore. Demarcation of the inshore area boundary is based on analysis of tag recoveries discussed in Laurs and Lynn (1977).

parameters, even though group-specific parameters are implied.)

In Model 1 we assume that the ratio of instantaneous growth rate, $dL(u)/du$, to potential growth, $L_\infty - L(u)$, is K, a constant. Instead, we may suppose generally that this ratio varies with age. We considered one such situation. In this model, Model 2, we assume that stresses due to capture, handling, and tagging will initially reduce the growth rate of a tagged fish below its usual level, but that as time passes the normal growth process will be restored. Specifically, in our analysis of Model 2 we assume the standard model holds for untagged fish but that when a fish is tagged its normal growth pattern is interrupted, such that

$$G(u) = K, \qquad 0 < u < t_{ij}$$

$$G(u) = K/\{1 + \alpha \exp[-\beta(u - t_{ij})]\} \qquad t_{ij} \leqslant u.$$

We assume $K \geqslant 0$, $\beta > 0$, and $\alpha \geqslant 0$. Model 2 says that following tagging the growth rate is immediately reduced to a fraction $(1 + \alpha)^{-1}$ of its normal value, K, and then returns to K asymptotically (Figure 1). L_∞ is assumed to be unaffected.

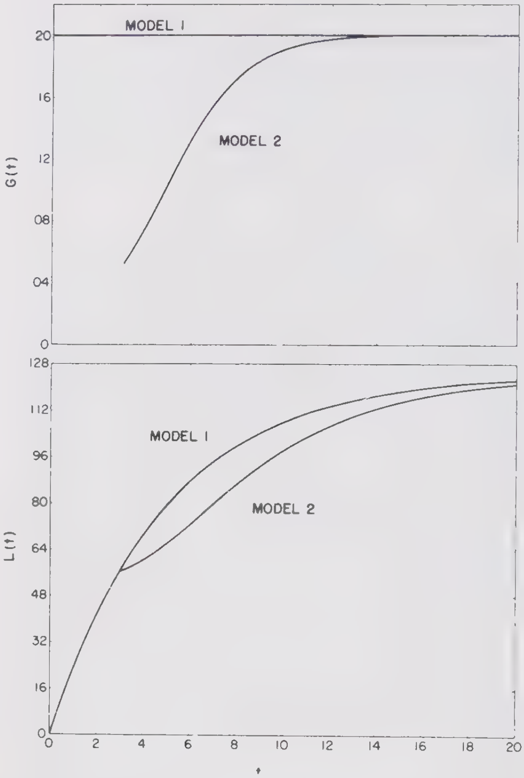

FIGURE 1.—Standard von Bertalanffy growth model (Model 1), and an extension (Model 2) incorporating a temporary reduction in growth rate, $G(t)$, following tagging. The resulting growth pattern, $L(t)$, is altered. Time units are arbitrary.

Parameter Estimation

In the standard von Bertalanffy model as applied to tag recapture data, there are two parameters to be estimated, K and L_∞. The usual approach is to estimate them simultaneously, and we did so using the FORTRAN program BGC 4 written by Tomlinson (1971). This routine finds $\hat{K}$ and $\hat{L}_\infty$ as those parameter values which minimize

$$S = \sum_{j=1}^{n_i} \left\{ L_{2_{ij}} - [L_\infty - (L_\infty - L_{1_{ij}}) \exp(-K\Delta_{ij})] \right\}^2,$$

where $L_{2_{ij}} = L(t_{ij} + \Delta_{ij})$. Since $E(L_{2_{ij}})$ is a nonlinear function of K, parameter estimates derived using this procedure are prone to serious bias unless observations on $L_{2_{ij}}$ are made over a wide range of $L_{1_{ij}}$ and Δ_{ij}. Presumably, it is also desirable that they be made uniformly in the plane of these two variables.

The parameters of Model 2 may also be estimated jointly using nonlinear least squares methods, but estimates of L_∞ and correlated parameters suffer the same drawbacks as estimates of the standard von Bertalanffy model parameters derived from BGC 4

An alternative approach in fitting both models is to estimate L_∞ and the other parameters sequentially. Where the oldest members of the population have been intensively sampled and an upper asymptote to length is clearly demonstrated in the data, a reasonable estimate of L_∞ is the length of the largest fish seen in the catches, or the average length of the largest specimens observed. Which estimator to use depends on one's conceptual model of the growth process—L_∞ can be regarded as the mean of a distribution of asymptotic lengths in the population, or strictly as an upper bound to the length any fish in the population can achieve. With the value of

L_∞ determined, the other parameters may be estimated by the least squares method using the general model:

$$Y_{ij} = -\ln\left(\frac{L_\infty - L_{2_{ij}}}{L_\infty - L_{1_{ij}}}\right) = \int_{t_{ij}}^{t_{ij}+\Delta_{ij}} G(u)\,du + \epsilon_{ij},$$

where we assume that ϵ_{ij} are independent errors with zero means and variances σ^2_{ij}.

This approach handily accommodates any well-behaved form of $G(u)$. In the case of Model 1, the problem of estimating K reduces to a simple linear regression:

$$Y_{ij} = K\Delta_{ij} + \epsilon_{ij}. \qquad (1)$$

When a reasonably accurate estimate of L_∞ can be made by sampling the catches, this sequential estimation procedure for Model 1 has the advantage that the range of observations on $L_{1_{ij}}$ and Δ_{ij} is not so critical.

With Model 2, the sequential method may be applied to estimate K, α, and β using the equation:

$$Y_{ij} = K\Delta_{ij} - \left(\frac{K}{\beta}\right)\ln\left\{(1+\alpha)/[1+\alpha\exp(-\beta\Delta_{ij})]\right\} + \epsilon_{ij}. \qquad (2)$$

The desirability of fitting this nonlinear model to any particular set of data may be judged by examining the residuals around the least squares fit of Model 1 (Equation (1)). As is evident from Figure 2, the detection of nonlinearity in this manner requires that observations be available uniformly over a broad range of Δ_{ij}.

Covariance Analysis

One of our chief objectives was to determine whether growth rates differed between groups of fish, based on estimates of parameters of the standard von Bertalanffy model. Since BGC 4 estimates of K and L_∞ are highly correlated, particularly when few large fish are in the sample, and since probability statements concerning intergroup comparisons of both K and L_∞ were not possible, we used the sequential estimation procedure. For the ith group of fish we assumed

$$E(Y_{ij}) = K_i\,\Delta_{ij}, \qquad (3)$$

where $Y_{ij} = -\ln\left(\dfrac{L_\infty - L_{2_{ij}}}{L_\infty - L_{1_{ij}}}\right)$

and specified a fixed value for L_∞. Then we developed and applied a weighted zero-intercept covariance analysis to test hypotheses of the form:

$$H: K_1 = K_2 = \ldots = K$$

on the basis of F-statistics. Statistical weights were computed on the assumption that $\sigma^2_{ij} \sim \Delta_{ij}$, as suggested by Figure 2.

RESULTS

Standard Model

Joint estimates of K and L_∞ for Groups A, B, and C, based on the BGC 4 program, are shown in Table 3. We consider the estimates inaccurate, owing to sampling biases discussed earlier. In particular, we think the unexpectedly low L_∞ estimates (and correspondingly high K estimates) are due to the absence of very large albacore in the release and recovery samples. Of the 410 selected tag returns, 141 exceeded 80 cm fork length at recapture, but only 42 were >85 cm and just 11 were >90 cm. The average fork length of tagged albacore at time of release was 63.7 cm (range 45-89 cm), and at recovery, 75.7 cm (range 51-103 cm).

Because of the difficulties with BGC 4 estimates, we based intergroup comparisons on estimates of K from the sequential estimation procedure. A preliminary F-test showed no significant difference in $\hat{K}$ between fish whose lengths at recovery were measured and those whose lengths were estimated from the inverted weight-length relationship. Further sequential analyses (as well as the earlier BGC 4 estimates) were therefore based on all data, regardless of how recovery length was determined.

L_∞ was fixed at 125 cm, a reasonable choice well supported by available length-frequency data. Although Otsu and Sumida (1970) reported an albacore measuring 132.7 cm from the

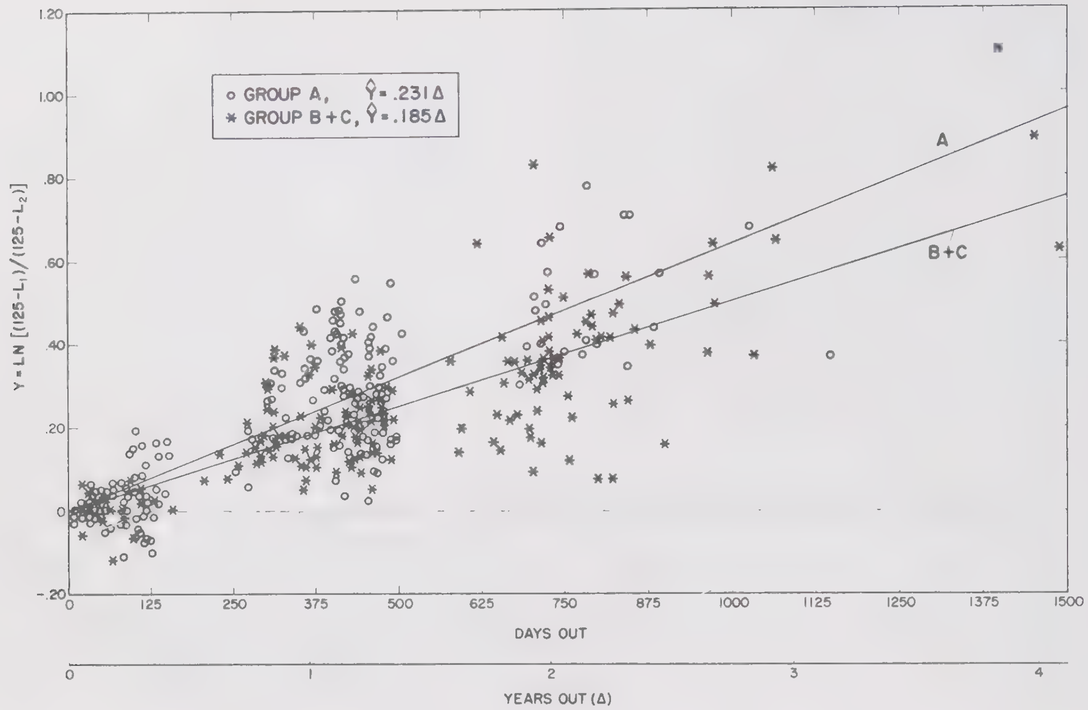

FIGURE 2.—Regression of growth variable, Y, on years between release and recapture for albacore of Groups A (221 fish) and B + C (189 fish). The slopes are estimates of the von Bertalanffy growth parameter, K, and they are significantly different.

TABLE 3.—Estimates of von Bertalanffy growth parameters for North Pacific albacore by recapture group and estimation method, assuming stock boundary at lat. 40° N.

Recapture group	Sample size	BGC4 estimates $\hat{L}_\infty$ (cm)	BGC4 estimates $\hat{K}$ (yr^{-1})	Sequential estimates Fixed L_∞ (cm)	Sequential estimates $\hat{K}$ (yr^{-1})	Average time out Δ (d)
A	221	94.5	0.505	125.0	0.231	313
B	75	107.5	.272	125.0	.193	400
C	114	98.5	.345	125.0	.184	588
B + C	189	102.1	.310	125.0	.185	513
A + B + C	410	100.9	.342	125.0	.199	405

Hawaiian longline fishery, which harvests the largest North Pacific albacore known, specimens >125 cm are extremely rare. With L_∞ fixed at 125 cm, Group A had the highest growth rate estimate, $\hat{K}_A = 0.231$/yr (Table 3). Group B and $\hat{K}_B = 0.193$, and Group C had the lowest growth rate estimate, $\hat{K}_C = 0.184$. When Groups B and C were pooled into a "North" category, the resulting $\hat{K}_N$ was 0.185. The estimate of K for all three groups combined was 0.199.

Table 3 also shows the statistics on average time between release and recapture. Group A fish were at liberty an average of 313 d, while Group B fish were out 400 d, and Group C fish, 588 d. Tagged fish from Groups B and C combined were at large an average of 513 d.

The estimates suggest that the North fish, Groups B and C, had a lower growth rate than the South fish of Group A. Such a difference might arise if, as we suppose, the North fish budget more of their available energy for migration compared with the South fish, and relatively less energy for growth. Tag release and recovery results indicate that the North fish make longer migrations, traveling between coastal waters off the United States Pacific Northwest and coastal waters off Japan, while the South fish undertake shorter migrations between coastal waters south of Cape

Mendocino, Calif., and the central North Pacific east of 180° (Laurs[6]).

The hypothesis of equal growth rates was tested using the weighted zero-intercept analysis of covariance, and was rejected at the 0.5% significance level (Table 4, Figure 2). In pairwise comparisons between individual groups, the only nonsignificant difference in growth rate was between Groups B and C.

Are the observed differences in growth rates of tagged albacore consistent with other information? To check this, we examined the length composition of albacore catches along the U.S. west coast (Figure 3). The length-frequency plot for catches north of lat. 38° N during the period when most recaptures were made, 1972-78, showed modes at about 64 and 76 cm and a hint of one at 54 cm. Catches south of lat. 38° N showed the 54 cm mode, but had primary modes at about 66 and 79 cm. The discrepancy between modes of the older albacore is further evidence of a slower growth rate for North fish, assuming these modes represent fish of the same age. To see if length-frequency data and tag data agreed, we computed the expected fork lengths under each $\hat{K}$ at annual time steps and compared these with observed modes in the length-frequency distributions. Starting with some initial fork length, L_1, we used the equation $L_i = a + bL_{i-1}$, $i = 2, 3, \ldots$, where $a = L_\infty\ (1 - \exp(-K))$ and $b = \exp(-K)$. Setting $L_1 = 54$ and $L_\infty = 125$ cm, we found the sequence of lengths 54.0, 66.0, and 76.0 cm for the North group albacore; and 54.0, 68.6, and 80.3 cm for the South fish. These are reasonably consistent with the observed sequences of length modes.

TABLE 4.—Analysis of covariance comparing growth rate of Group A North Pacific albacore with growth rate of Group (B + C) albacore, assuming stock boundary at lat. 40° N. Probability of obtaining F statistic this large under null hypothesis is <0.005.

Source of variation	df	Residual SS	MS	F
Individual lines:				
A	220	1.1476		
B + C	188	1.7362		
Pooled	408	2.8837	0.0071	
Common line	409	3.1009		
Difference	1	.2172	.2172	30.72

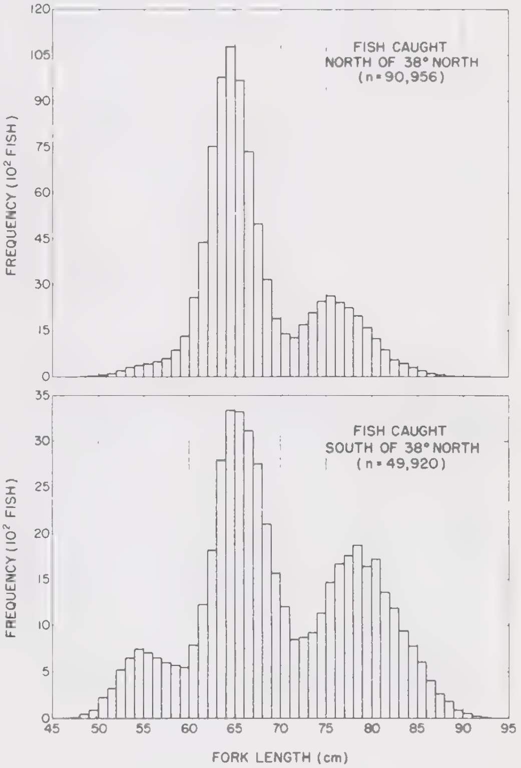

FIGURE 3.—Composite length-frequency distributions for North Pacific albacore caught north of lat. 38° N and south of lat. 38° N off the U.S. west coast during the 1972-78 fishing seasons.

Extended Model

Plots of residuals from the standard model against days out (Figure 4) showed a tendency toward negative deviations during the first several months after tagging, suggesting that some of the residual variation could be attributed to "lack of fit" (Draper and Smith 1966). For example, of the 221 recaptures analyzed in Group A, 90 were taken within 6 mo of tagging, and 70% of the Model 1 residuals corresponding to these early recaptures were negative. We therefore fit Model 2 to each set of data, using the sequential estimation procedure (Equation (2)) with $L_\infty = 125$ cm. Resulting estimates of K were 3-6% larger than the corresponding estimates from the standard linear model; thus, if Model 2 is correct, systematic bias in the latter estimates does not appear to be serious.

However, estimates of α and β were relatively large in all cases, suggesting that the growth rate may drop abruptly to near zero immediately after

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[6] Laurs, R. M. 1979. Results from North Pacific albacore tagging studies. Southwest Fish. Cent. La Jolla Lab., Natl. Mar. Fish. Serv., NOAA, Admin. Rep. LJ-79-17, 10 p.

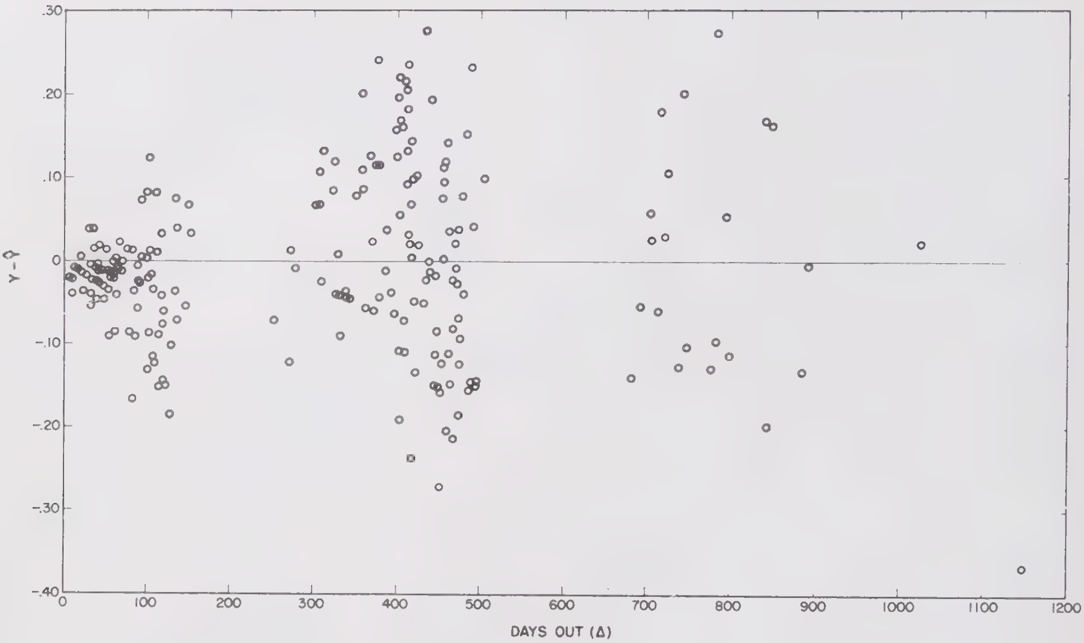

FIGURE 4.—Residuals from the fit of Model 1 to the Group A albacore data, as a function of days out.

tagging and then recover to normal within the first year of liberty. While this basic response to tagging stress appears to be a reasonable hypothesis, the estimates of α and β were very unstable and little confidence could be placed on projected growth rate recovery patterns. Further, although the extended model fits the data better than the ordinary von Bertalanffy in the sense of reducing residual variation, as expected, this improvement is only slight; considering the high variance displayed in the data we do not reject the simpler von Bertalanffy model.

DISCUSSION AND CONCLUSIONS

The results of our growth analysis are strengthened by their consistency with other findings, but the assumptions of our analysis need to be tested. In particular, we assumed that our estimate of L_∞, 125 cm, was the same for all groups of North Pacific albacore. If $L_\infty(\mathrm{B + C}) > L_\infty(\mathrm{A})$, our conclusions concerning differences in growth rate are reinforced. But if the South fish, Group A, actually tend toward a larger asymptote in fork length than the North fish of Groups B and C (there is no evidence of this), then the differences between estimates of K might not be significant. For example, if we assume $L_\infty(\mathrm{A}) = 130$ cm and $L_\infty(\mathrm{B + C}) = 120$ cm, the differences vanish. More to the point, unless the L_∞'s are the same, the comparison of growth rates between groups is no longer conveniently reduced to a comparison of K estimates. When the assumption of equal L_∞ is valid, the actual value of L_∞ assumed is relatively unimportant as far as the covariance analysis is concerned; our conclusions were the same when L_∞ was fixed at 120, 130, and 135 cm.

In Model 1, the standard von Bertalanffy model, we also assumed that the growth rate was unaltered by the presence of the tag or by the stress imposed in its application. In our analysis of Model 2 we explored the question of whether tagging might have affected growth rate in a specified way, and Model 2 fits our data only slightly better than Model 1. However, effects of the sort we hypothesized might easily be masked by high variance in the data. Nevertheless, if the effect of tagging were simply to reduce the normal growth rate, K, suddenly and permanently to a lower level, K', it would go undetected by our analysis. To determine the validity of the tag-effect assumption, we need to compare the growth rates of tagged fish with those of untagged, "control" fish.

Such a comparison was recently made for baitboat-caught southern bluefin tuna, *T. maccoyii*, by Hearn,[7] who found that fish caught 3 wk after being tagged weighed 14% less than untagged fish of the same length in the same schools. Assuming the tagged bluefin tuna also grew less in length than their untagged counterparts, this 14% weight loss would be an underestimate. At any rate, after 1 yr at liberty no difference in weight was discernible.

We found that the growth rate of North Pacific albacore recaptured either off the coast of North America north of lat. 40° N or in the western North Pacific off Japan was significantly lower than for tagged albacore recaptured off North America south of lat. 40° N during 1972-78. The differences in growth rate of tagged fish are remarkably consistent with differences in length-frequency distributions of albacore caught off North America north and south of lat. 38° N during the period when most recaptures were made. These findings add to a growing body of evidence (Brock 1943; Laurs and Lynn 1977; Laurs et al.[8]; Laurs and Lynn[9]) that North Pacific albacore are not as homogeneous as usually assumed, and that there may be at least two subgroups of albacore: one which supported the Japanese pole-and-line fishery and the United States and Canadian fisheries in waters north of about lat. 40° N from 1972 to 1978, and another which did not contribute significantly to the Japanese surface fishery, but supported the United States coastal fishery south of lat. 40° N during this period. If such a distinction is valid, the situation is surely more complex and dynamic than we have supposed, with each stock's contribution to each fishery varying from year to year. Presumably such variation would be tied directly to changes in oceanographic conditions. And undoubtedly the latitudinal boundary was not fixed exactly at lat. 40° N during 1972-78, as we assumed, but analyses based on assumed boundaries at lat. 38° and 42° N gave the same results. If an accurate assignment of tagged fish to stock were possible, a more powerful test of growth differences could be made.

A finding that more than one subpopulation or stock is involved in the North Pacific albacore fisheries would have important consequences, of course, both for stock assessment, fishery evaluation and management policy analysis, and for development of accurate catch forecasting systems. It is important that further work be done to identify stocks, and to elucidate their origins, migratory habits, and degree of interchange.

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Sea surface temperatures in the northwestern Atlantic in 1979

(Figures 36-50; Table 3)

Sea surface temperature (SST) data, principally collected from cooling water intakes of merchant ships, are reported in radio weather messages and log books transmitted to the U.S. Fleet Numerical Oceanography Center (FNOC) and the National Climatic Center for processing and archiving. The "real-time" reports of the data base provided by the radio messages are analyzed by FNOC and the Pacific Environmental Group of the National Marine Fisheries Service, which is co-located with FNOC. An elementary step in the analysis is the computation of average monthly temperatures and anomalies (from 1948-1967 means) for each 1° × 1° square for which at least 2 observations have been reported each month. The average SSTs, anomalies, and number of observations are then printed in the 1° × 1° squares they characterize to produce a map such as the one shown in Figure 36. To facilitate interpretation of the data, anomalies greater than +1°C or less than −1°C are shaded.

Monthly maps of this sort for the northwestern Atlantic for 1979 (Figs. 36-47) reveal that an area of colder-than-average water developed throughout the western section from Cape Hatteras to Nova Scotia in February, weakened slightly in March, and disintegrated in April. The weather changes which produced this sequence are clearly shown in meteorological data collected at coastal weather stations. For example, data from the Boston, Massachusetts, station showed that below-normal air temperatures occurred in February (4·1°C colder than normal) and were accompanied by vigorous westerly winds (average speed 8·1 m/sec). This combination of factors caused a strong flow of cold, dry air over coastal waters and caused rapid cooling of the surface water. In March more moderate weather conditions prevailed, particularly during the last 10 days of the month. The

Table 3. Anomalies of monthly mean sea surface temperature (°C) from the long-term mean (1948–1967) for 1979 in the northwestern Atlantic Ocean (35°–46°N 60°–76°W)

Month	Number of 1°-squares	Area mean anomaly	Standard deviation of area mean anom. 1948-1967
Jan	117	−0·18	1·26
Feb	109	−0·80	1·23
Mar	121	−0·35	1·49
Apr	126	+0·20	1·51
May	133	+0·60	1·22
Jun	130	+0·65	0·91
Jul	127	−0·39	0·89
Aug	126	0·00	0·85
Sep	128	+0·29	0·89
Oct	126	−0·02	0·95
Nov	121	+0·42	0·90
Dec	105	+0·28	0·91

Figures 36-47. Average sea surface temperature anomalies (°C). Also shown in each one-degree square are average sea surface temperatures (upper number) and the number of observations (lower number).

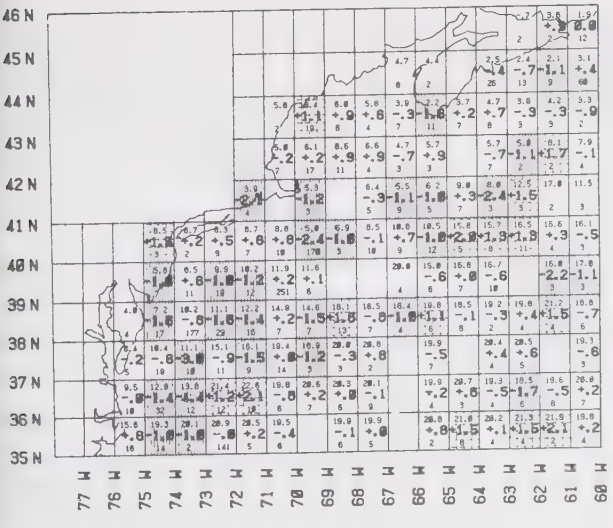


Figure 36. January 1979.

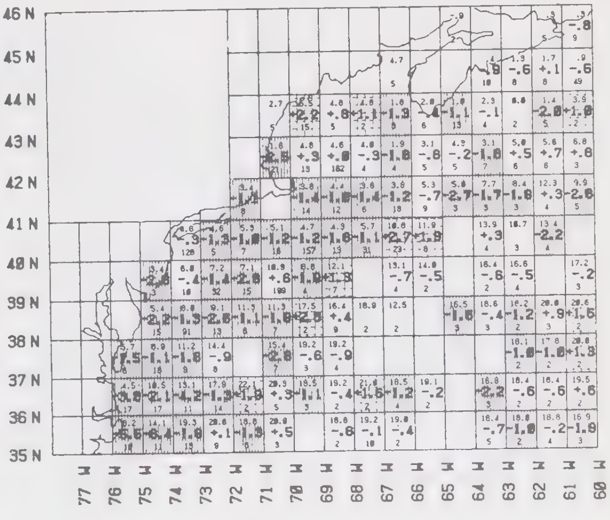


Figure 37. February 1979.

average air temperature in March was 2·4°C above normal with weaker westerly winds (average speed 6·6 m/sec). The moderation in weather continued in April, with nearly average air temperatures and less vigorous winds, which became southerly during the last third of the month.

The most unusual occurrence in the surface layer temperature field in 1979, however, was the development of a band of warm temperature anomalies between 38° and 40°N in the western section in May (Fig. 40). One month later, in June, this band appears to have shifted northward and broadened to occupy the area between 41° and 46°N. By July the area of positive anomalies disintegrated except for a small region southwest of Nova Scotia. The link between this anomaly and coastal meteorological conditions was not as apparent as was the case in winter.

In order to characterize the SST of the entire area

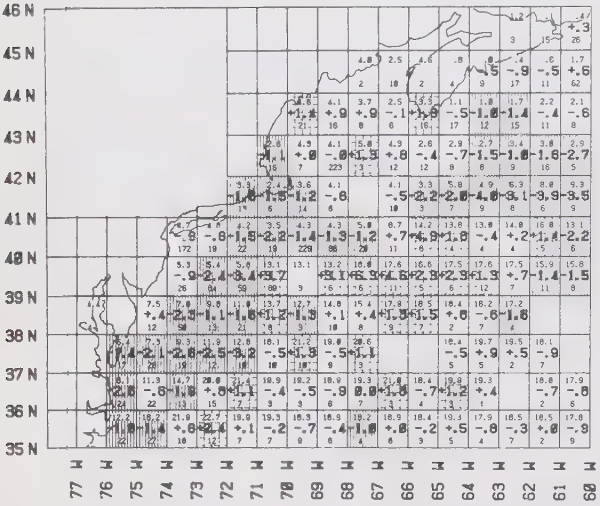


Figure 38. March 1979.

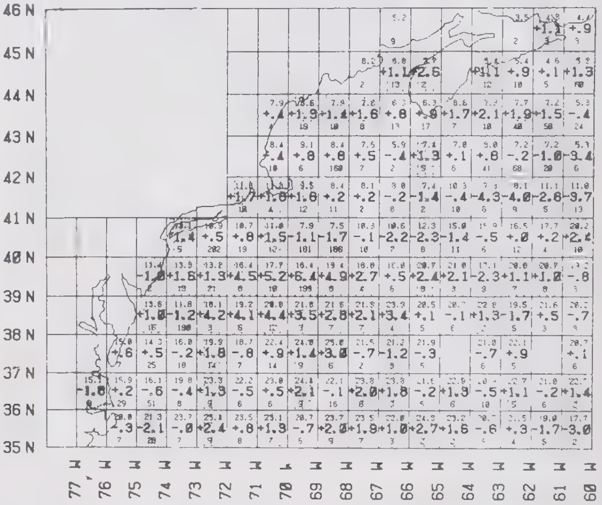


Figure 40. May 1979.

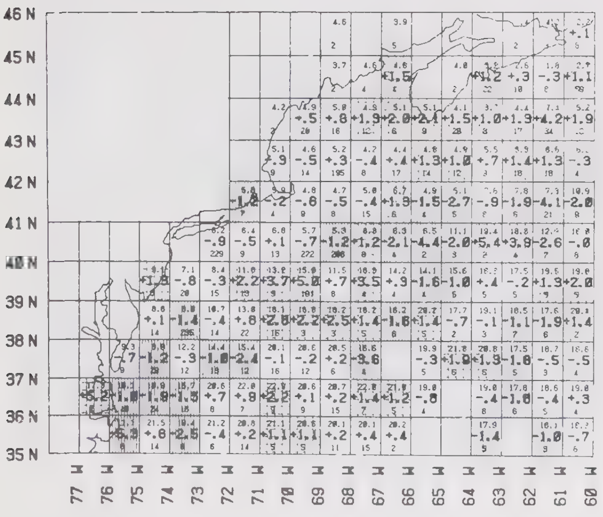


Figure 39. April 1979.

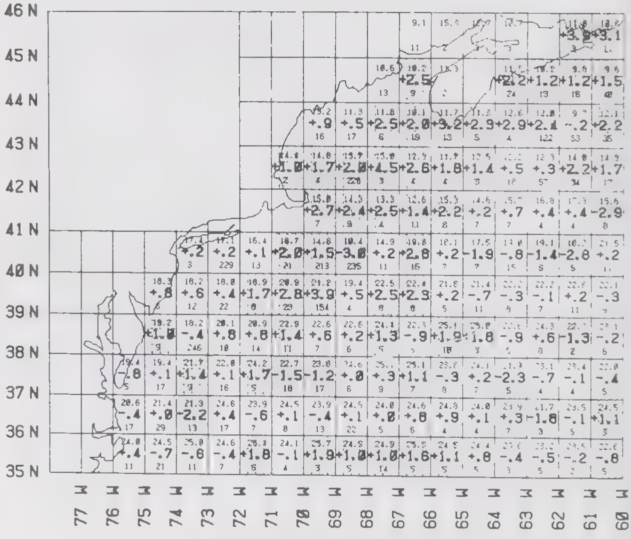


Figure 41. June 1979.

(35°-46°N 60°-76°W) with a single number, the mean of all the mapped anomalies was computed for each month. The resulting monthly area means (Table 3) show a strongly negative value only in February and strongly positive ones in May and June.

Spatial and temporal gradients of SST in the nearshore shelf waters can be portrayed by plotting the monthly anomalies from selected coastal one-degree squares on a space-time grid. Figure 48 is a plot such as this for 15 one-degree squares between Cape Hatteras and Nova Scotia for 1979 (Fig. 49). The plot clearly shows the widespread effect of the cooling which took place in late January and February; all 15 squares showed negative anomalies in February. The anomalously cold water appears to have persisted longer in the southern squares (13-15) than in the others. The development of warmer-than-usual water in April-July occurred in the northern squares only.

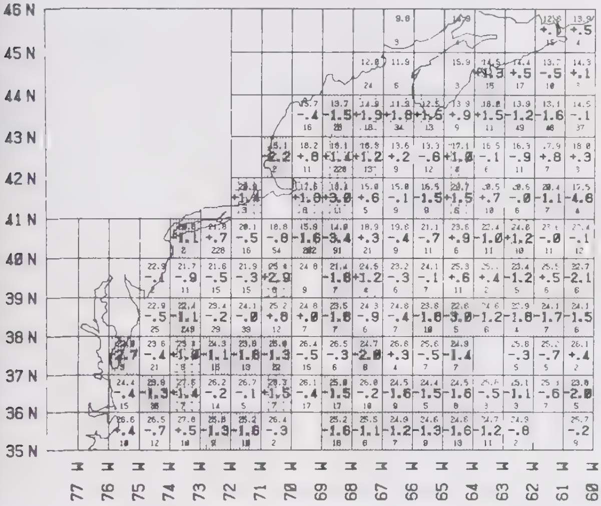


Figure 42. July 1979.

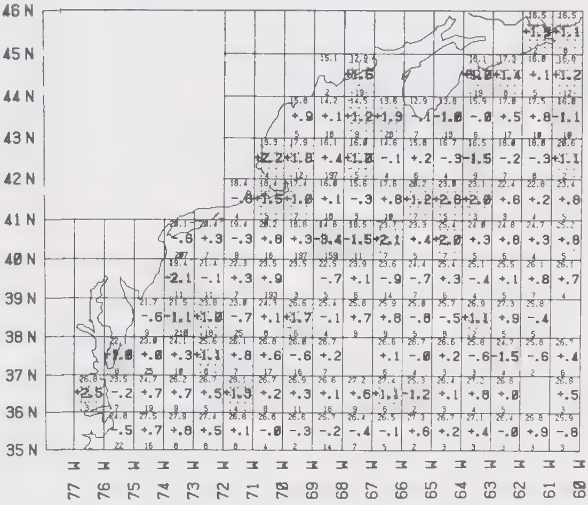


Figure 44. September 1979.

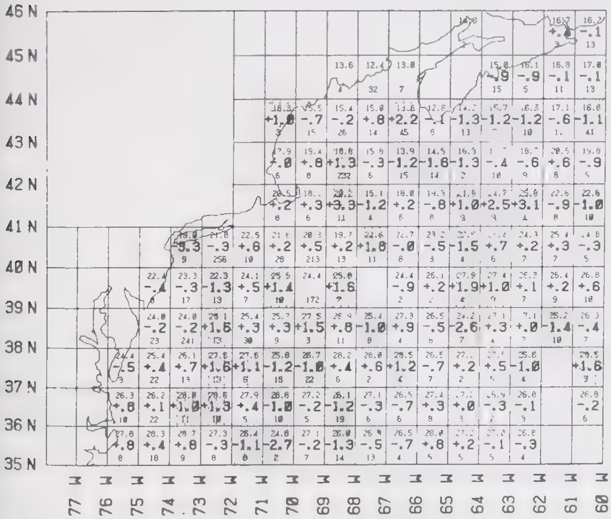


Figure 43. August 1979.

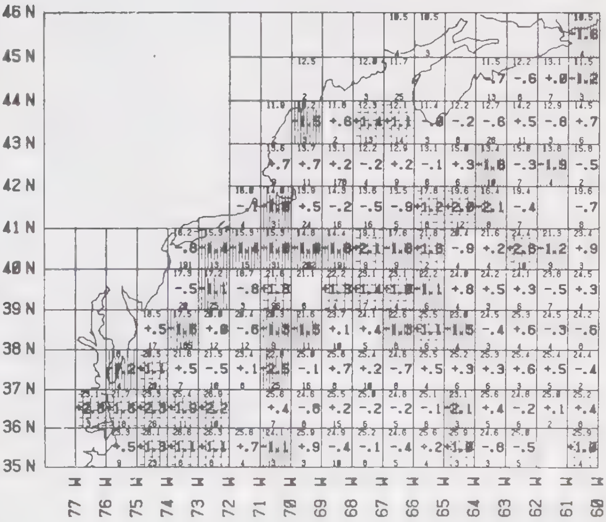


Figure 45. October 1979.

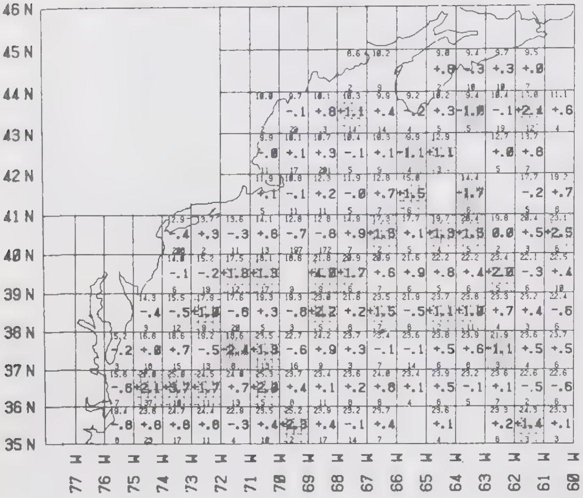


Figure 46. November 1979.

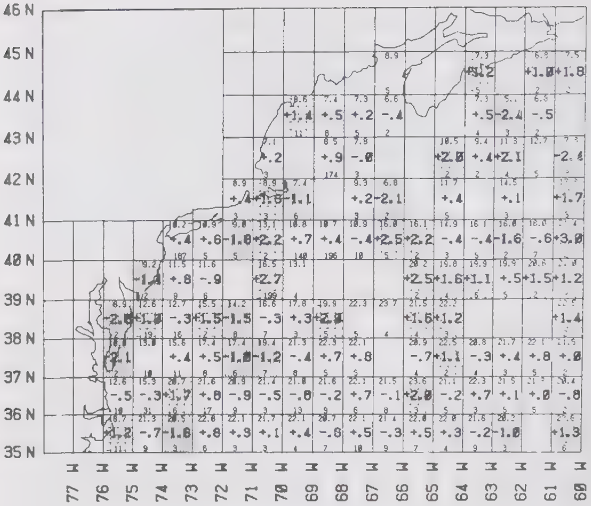
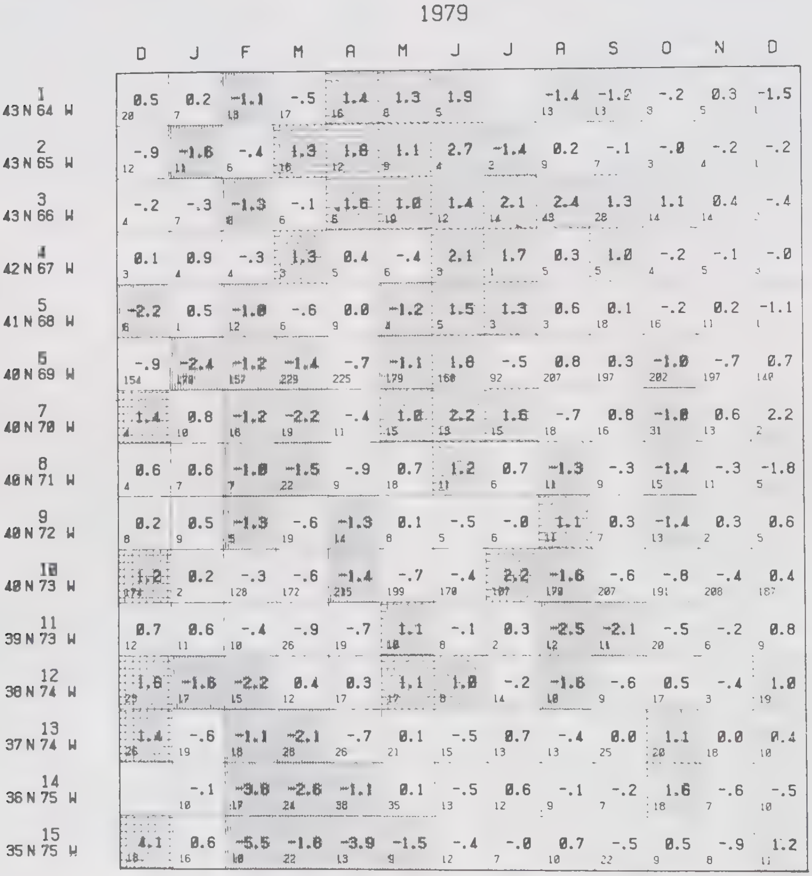


Figure 47. December 1979.



1979

	D	J	F	M	A	M	J	J	A	S	O	N	D
1 43 N 64 W	0.5 20	0.2 7	-1.1 18	-.5 17	1.4 16	1.3 8	1.9 5		-1.4 13	-1.2 13	-.2 3	0.3 5	-1.5 1
2 43 N 65 W	-.9 12	-1.6 11	-.4 6	1.3 16	1.8 12	1.1 9	2.7 4	-1.4 2	0.2 9	-.1 7	-.0 3	-.2 4	-.2 1
3 43 N 66 W	-.2 4	-.3 7	-1.3 8	-.1 6	1.6 5	1.0 10	1.4 12	2.1 14	2.4 43	1.3 28	1.1 14	0.4 14	-.4 [illegible]
4 42 N 67 W	0.1 3	0.9 4	-.3 4	1.3 3	0.4 5	-.4 6	2.1 3	1.7 1	0.3 5	1.0 5	-.2 4	-.1 5	-.0 3
5 41 N 68 W	-2.2 6	0.5 1	-1.0 12	-.6 6	0.0 9	-1.2 4	1.5 5	1.3 3	0.6 3	0.1 18	-.2 16	0.2 11	-1.1 1
6 40 N 69 W	-.9 154	-2.4 170	-1.2 157	-1.4 229	-.7 225	-1.1 179	1.8 160	-.5 92	0.8 207	0.3 197	-1.0 202	-.7 197	0.7 140
7 40 N 70 W	1.4 4	0.8 10	-1.2 16	-2.2 19	-.4 11	1.0 15	2.2 13	1.6 15	-.7 18	0.8 16	-1.0 31	0.6 13	2.2 2
8 40 N 71 W	0.6 4	0.6 7	-1.0 7	-1.5 22	-.9 9	0.7 18	1.2 11	0.7 6	-1.3 11	-.3 9	-1.4 15	-.3 11	-1.8 5
9 40 N 72 W	0.2 8	0.5 9	-1.3 5	-.6 19	-1.3 14	0.1 8	-.5 5	-.0 6	1.1 11	0.3 7	-1.4 13	0.3 2	0.6 5
10 40 N 73 W	1.2 174	0.2 2	-.3 128	-.6 172	-1.4 215	-.7 199	-.4 170	2.2 187	-1.6 178	-.6 207	-.8 191	-.4 208	0.4 187
11 39 N 73 W	0.7 12	0.6 11	-.4 10	-.9 26	-.7 19	1.1 18	-.1 8	0.3 2	-2.5 12	-2.1 11	-.5 20	-.2 6	0.8 9
12 38 N 74 W	1.6 29	-1.6 17	-2.2 15	0.4 12	0.3 17	1.1 17	1.0 8	-.2 14	-1.6 10	-.6 9	0.5 17	-.4 3	1.0 19
13 37 N 74 W	1.4 26	-.6 19	-1.1 18	-2.1 28	-.7 26	0.1 21	-.5 15	0.7 13	-.4 13	0.0 25	1.1 20	0.0 18	0.4 10
14 36 N 75 W		-.1 10	-3.8 17	-2.6 24	-1.1 38	0.1 35	-.5 13	0.6 12	-.1 9	-.2 7	1.6 18	-.6 7	-.5 10
15 35 N 75 W	4.1 18	0.6 16	-5.5 10	-1.8 22	-3.9 13	-1.5 9	-.4 12	-.0 7	0.7 10	-.5 22	0.5 9	-.9 8	1.2 11

Figure 48. Space-time plot of sea surface temperature anomalies (°C) for 1979. Also shown are the numbers of observations utilized (lower left corner of squares). Location of one-degree squares (1-15) shown in Figure 49.

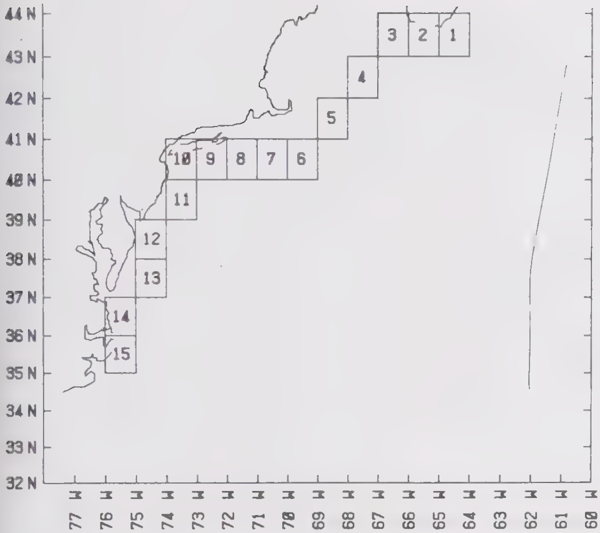


Figure 49. Location of one-degree squares of interest utilized in Figures 48 and 50 (Nova Scotia-Cape Hatteras).

In contrast with the 1979 conditions, those in 1978 (Fig. 50) led to the development of a long-lasting (February-July) band of negative anomalies in the southern half of the area (squares 6-15), but only weak positive anomalies appeared in the July-November period.

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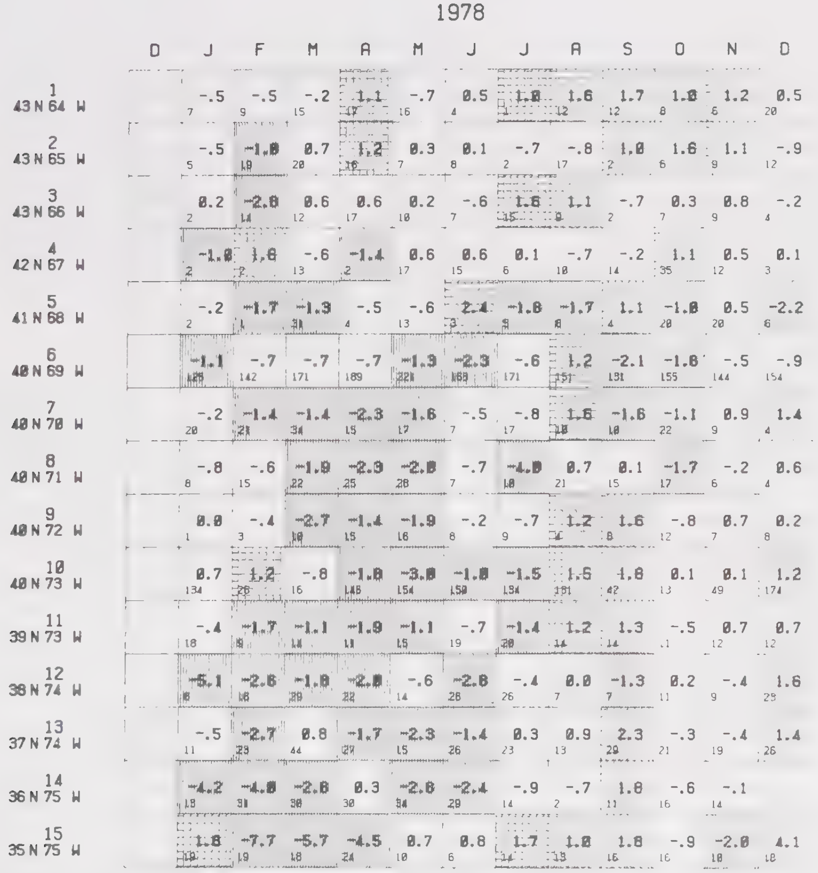

1978

	D	J	F	M	A	M	J	J	A	S	O	N	D
1 43 N 64 W		-.5 7	-.5 9	-.2 15	1.1 17	-.7 16	0.5 4	1.0 1	1.6 12	1.7 12	1.0 8	1.2 6	0.5 20
2 43 N 65 W		-.5 5	-1.0 10	0.7 20	1.2 16	0.3 7	0.1 8	-.7 2	-.8 17	1.0 2	1.6 6	1.1 9	-.9 12
3 43 N 66 W		0.2 2	-2.0 14	0.6 12	0.6 17	0.2 10	-.6 7	1.6 15	1.1 9	-.7 2	0.3 7	0.8 9	-.2 4
4 42 N 67 W		-1.0 2	1.6 2	-.6 13	-1.4 2	0.6 17	0.6 15	0.1 6	-.7 10	-.2 14	1.1 35	0.5 12	0.1 3
5 41 N 68 W		-.2 2	-1.7 1	-1.3 31	-.5 4	-.6 13	2.4 3	-1.0 9	-1.7 8	1.1 4	-1.0 20	0.5 20	-2.2 6
6 40 N 69 W		-1.1 128	-.7 142	-.7 171	-.7 189	-1.3 221	-2.3 169	-.6 171	1.2 151	-2.1 131	-1.6 155	-.5 144	-.9 154
7 40 N 70 W		-.2 20	-1.4 21	-1.4 34	-2.3 15	-1.6 17	-.5 7	-.8 17	1.6 10	-1.6 10	-1.1 22	0.9 9	1.4 4
8 40 N 71 W		-.8 8	-.6 15	-1.9 22	-2.3 25	-2.0 20	-.7 7	-4.0 10	0.7 21	0.1 15	-1.7 17	-.2 6	0.6 4
9 40 N 72 W		0.0 1	-.4 3	-2.7 10	-1.4 15	-1.9 16	-.2 8	-.7 9	1.2 4	1.6 8	-.8 12	0.7 7	0.2 8
10 40 N 73 W		0.7 134	1.2 26	-.8 16	-1.0 146	-3.0 154	-1.0 150	-1.5 134	1.5 101	1.8 42	0.1 13	0.1 49	1.2 174
11 39 N 73 W		-.4 18	-1.7 9	-1.1 14	-1.9 11	-1.1 15	-.7 19	-1.4 20	1.2 14	1.3 14	-.5 1	0.7 12	0.7 12
12 38 N 74 W		-5.1 8	-2.6 16	-1.0 20	-2.0 22	-.6 14	-2.8 26	-.4 26	0.0 7	-1.3 7	0.2 11	-.4 9	1.6 23
13 37 N 74 W		-.5 11	-2.7 23	0.8 44	-1.7 27	-2.3 15	-1.4 26	0.3 23	0.9 13	2.3 20	-.3 21	-.4 19	1.4 26
14 36 N 75 W		-4.2 18	-4.0 31	-2.8 30	0.3 30	-2.8 34	-2.4 29	-.9 14	-.7 2	1.8 11	-.6 16	-.1 14	
15 35 N 75 W		1.8 10	-7.7 19	-5.7 18	-4.5 24	0.7 10	0.8 6	1.7 14	1.0 13	1.8 16	-.9 16	-2.0 10	4.1 18

Figure 50. Space time plot of sea surface temperature anomalies (°C) for 1978. Also shown are the numbers of observations utilized (lower left corner of squares). Location of one-degree squares (1-15) shown in Figure 49.

Expendable Bathythermograph Sections, 1972-79

Temperature profiles are made at irregular intervals of time throughout the Pacific Ocean along standard ship routes using expendable bathythermographs (XBT) deployed from ships-of-opportunity. Since 1972 NOAA's Pacific Environmental Group (PEG) has processed and archived these data. The data, initially received in analog trace form, are digitized and processed utilizing the Navy's Fleet Numerical Oceanography Center's (FNOC) computer facilities. Various computer products utilizing these data are available to interested scientists including tape copies of the digitized measurements. Data recorded from 1972 to 1979 between about 20°N and the equator between 140°W and 180° (Figure 1) will be used to describe the time-variations of the transport of the North Equatorial Current (NEC) between ~ 11°N and 20°N and the transport of the North Equatorial Countercurrent (NECC) (usually found between 4°N and 11°N). These data provide a continuation of the Wyrtki *et al.* (1977) measurements.

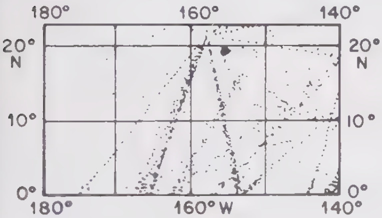

FIGURE 1 (*McLain & Favorite*)
Location of XBT data.

Because of the intense thermocline in the equatorial waters, the ocean can be approximated as a 2-layer system with the lower layer at rest. Wyrtki and Kendall (1967) showed that for such a simplified case, it is possible to estimate the transports of the currents using only the depths of selected isotherms in the thermocline near the northern and southern edges of each current and the density difference between the upper and lower layers. The equation contains two terms: the depth difference of the isotherm across the current (related to the slope of the thermocline), and the mean depth of the isotherm (related to the thickness of the surface layer). Time variations of the transport computed from each individual XBT section are shown in Figure 2. The mean annual cycles of the transports were computed from an average of the monthly values shown in Figure 2.

The mean depth of the 14°C isotherm in the NEC varied from 153 m in August to 209 m in January, the mean depth difference (slope of the isotherm) varied from 103 m in July to 176 m in January, and the resulting monthly mean transport varied from 11.4 Sv (1 Sv = 1 x 10^6 m^3 s^{-1}) in July to 24.2 SV in January (Figure 2A). This compared with a range of individual transports of 13.8 Sv to 19.1 Sv found by Wyrtki *et al.* (1977). The greater range found in this study may be due to the increased number of XBT sections now available.

The mean depth of the 20°C isotherm in the NECC was relatively constant, varying from 99 m in April to 123 m in January, the mean depth difference (slope) varied from 43 m in July to 111 m in November, and the mean transport varied from 11.2 Sv in July to a peak of 32.5 Sv in November (Figure 2B).

We believe that these data adequately re-

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Low Frequency Variability in the Atlantic

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and $\left\{\partial\sigma/=(gh)^{1/2}\right\}$ and $\left\{\partial\sigma/\partial m=\sigma(gh)^{1/2}/N\right\}$, for Kelvin waves, where σ is wave frequency, *k* is horizontal wavenumber, *m* is vertical wavenumber and *N* is buoyancy frequency. Using the scales from Figure 3, Table 1 gives component estimates, travel times to the observational depth, and zonal distance traversed.

TABLE 1 (*Weisberg & Horigan*)

Group velocity component estimates for long and short Rossby waves and for a Kelvin wave (using values from Figure 3), the associated travel times for energy to propagate 1000 m vertically with $N = 0.002\ s^{-1}$, and the corresponding zonal distance traversed during this time.

	$\frac{\partial\sigma}{\partial k}$ cm s^{-1}	$\frac{\partial\sigma}{\partial m}$ cm s^{-1}	ΔT (1000 m) days	ΔX km
Long	− 3.0	-2.2×10^{-3}	526	−1390
Short	+ 0.5	-3.6×10^{-4}	3215	1360
Kelvin	+14.0	-2.5×10^{-3}	463	5600

Kelvin waves, if generated near the surface in the western Atlantic, travel sufficiently fast to reflect off an eastern boundary becoming long Rossby waves before reaching the observational depth. Therefore, a predominance of linear Kelvin waves seems unlikely. Long and short Rossby waves have oppositely directed zonal group speeds. For a given vertical distance they traverse similar zonal distances with the longer waves moving much faster. Short Rossby waves arriving at the observational site would be generated in the central portion of the Atlantic since their energy flux is eastward.

An interesting finding is the relatively narrow vertical wavenumber bandwidth. Generation of narrow band waves by reflection is not expected, whereas generation by wave drag or instability would be expected to produce narrow band packets. Short Rossby waves are consistent with this type of generation since the eastward directed Equatorial Undercurrent is the principal momentum source on the equator.

Regardless of the above conjectures, a significant problem exists. The maximum zonal phase speeds for Kelvin and long Rossby waves are $(gh)^{1/2}$ and $(gh/3)^{1/2}$ respectively. Short Rossby waves are slower. Given the small observed vertical scales, with $(gh)^{1/2} = 14\ cm\ s^{-1}$, relative to the observed *u* component amplitudes, it appears that the low frequency zonal oscillations are intrinsically nonlinear (also suggested by Eriksen, 1980).

In summary, statistically and physically distinct low frequency *v* and *u* component behavior has been observed. The *v* component oscillations appear as linear, seasonally modulated expressions of nonlinearly induced waves. The *u* component oscillations appear as nonlinear features of unknown origin. Zonal scale information as well as theoretical guidance is needed.

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SST Fronts and Eddies

from page 13

PAX drifting buoys were deployed in the central Pacific (Patzert and McNally, see *TO-AN No. 3*, July 1980) some of which drifted along with the NECC. All buoys displayed wave-like trajectories except buoy 2807 which became trapped in an eddy-like clockwise circulation for approximately 45 days. Our SST analysis shows an anomalous high in the same region at the same time, suggesting the existence of a gyre. Figure 3 shows the station data (dots), SST contours (solid lines), and part of the buoy tracks (dashed lines). Unfortunately, there is not enough data in hand to explain convincingly the coincidence between the SST-anomalies and the eddy-like buoy tracks, but the data suggest the existence of eddies in the region between the SEC and the NECC.

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Index

An index of the contents and contributors to the first year's editions of the newsletter follows on page 15. The January issue of TO-AN will regularly feature an index of the previous year's manuscripts and authors.

The Editors

Expendable Bathythermographs

from page 7

solve the mean annual cycle of the transports of the NEC and the NECC. Sampling density is insufficient, however, to adequately resolve interannual fluctuations such as the effects of the El Niño phenomena. Sampling for several years at the rate obtained in 1979 would probably be necessary to resolve such interannual fluctuations.

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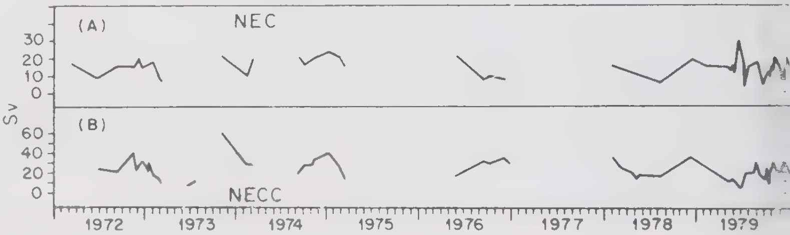

FIGURE 2 (*McLain & Favorite*)
Transports of the (A) North Equatorial Current and the (B) North Equatorial Countercurrent.

MEETINGS

EPOCS Meeting, 3-5 February 1981, Boulder Colorado

The third annual meeting of the EPOCS Co-Principal Investigators, 3-4 February, and the fourth annual meeting of the EPOCS Advisory Panel, 5 February, will be held in Boulder. Contact: Dr. Kent L. Groninger, Office of Programs, Environmental Research Laboratories, NOAA, Boulder, Colorado 80303 (tel: 303-449-1000-ext 6212).

SCOR WG 47, FGGE Oceanography, 27-30 April 1981, Venice, Italy

Reseachers will report oceanographic results found in the equatorial Atlantic, Indian and Pacific Oceans during the Global Weather Experiment. Similarities and differences of the equatorial regions will be highlighted. Contact: Dr. Jay McCreary, Nova University Ocean Sciences Center, 8000 North Ocean Drive, Dania, Florida 33004 (tel: 305-475-7487).

SCOR WG 56, Equatorial Upwelling Processes, 5-7 May 1981, Paris, France

The second combined meeting of the Biological and Physical Panels will be held 5-7 May 1981 in Paris, France. Contact: Dr. Henri Rotschi, Centre de Recherches Oceanographiques, ORSTOM, 29 Rue des Pecheurs, B.P.V. 18, Abidjan, Ivory Coast (tel: 35-50-14).

Notices

A bibliography of research on the ph nomenon of upwelling has been prepared b Dr. A.F. Anto and Dr. V.V.R. Varadachar This bibliography contains most of the publ cations on physical, chemical, biological an geological aspects of upwelling published be tween 1890 and 1977. Please send requests t Dr. A.F. Anto, National Intstitute of Ocean ography, Dona Paula, 403 004 Goa, India.

A bibliography of research on the physi cal processes in the equatorial regions of th oceans has been compiled by Ms. Janet Witte Please send requests to Ms. Janet Witte, Nov University Ocean Sciences Center, 800 North Ocean Drive, Dania, Florida 33004.

The **Tropical Ocean-Atmosphere Newsletter (*TO-AN*)** is published quarterly with support by NOAA's Equatorial Pacific Ocean Climate Studies program and edited by David Halpern and Beverly Jensen Katirayi.

Material for publication may be sent to Dr. David Halpern, NOAA Pacific Marine Environmental Laboratories, 3711 15th Ave. N.E., Seattle, Washington 98105. Material included in the newsletter is not to be quoted or published without the permission of the contributing scientist. In citing this newsletter in a bibliography, the reference should be followed by the phrase "Unpublished manuscript."

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SEASONAL GROWTH PATTERNS OF CALIFORNIA STOCKS OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, PACIFIC MACKEREL, *SCOMBER JAPONICUS*, AND JACK MACKEREL, *TRACHURUS SYMMETRICUS*

DONNA L. MALLICOATE AND RICHARD H. PARRISH
Pacific Environmental Group
Southwest Fisheries Center
National Marine Fisheries Service
National Oceanic and Atmospheric Administration
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ABSTRACT

Market sample data obtained from the California Department of Fish and Game were analyzed to show number, mean length, and mean weight of fish by age and month for northern anchovy, *Engraulis mordax*, Pacific mackerel, *Scomber japonicus*, and jack mackerel, *Trachurus symmetricus*. In addition, maximum and minimum lengths and weights and their standard deviations were calculated.

Graphs showing the relationship between age and length and between age and weight were produced for each of these three species. The graphs show that the age-length relationships of Pacific mackerel, jack mackerel, and northern anchovy landed in southern California and of northern anchovy landed in central California are adequately described by the von Bertalanffy growth curve. These graphs also show considerable seasonal variation in the age-weight relationships. These seasonal fluctuations may be related to the occurrence of spawning and feeding relationships. Analysis of the growth in weight suggests that a size limit would be expected to increase yields of Pacific mackerel, but not of jack mackerel or northern anchovy.

RESUMEN

Datos de muestras de anchoveta del norte, *Engraulis mordax*, macarela, *Scomber japonicus*, y macarela caballa, *Trachurus symmetricus*, colectadas en el mercado por el California Department of Fish and Game, se analizaron para mostrar número, longitud media, y peso medio de los peces por edad y por mes. Adicionalmente, se calcularon las longitudes y los pesos máximos y mínimos y sus desviaciones estándard.

Se produjeron gráficas para cada una de estas tres especies, mostrando la relación entre edad y longitud y entre edad y peso. Las gráficas muestran que para la macarela, macarela caballa y anchoveta del norte desembarcadas en el sur de California, y para la anchoveta del norte desembarcada en California central, las relaciones entre edad y longitud están descritas adecuadamente por la curva de crecimiento de von Bertalanffy. Estas gráficas también muestran considerable variación estacional en las relaciones entre edad y peso. Estas variaciones estacionales pueden estar relacionadas con desove y alimentación. El análisis del crecimiento en peso sugiere que con un tamaño límite se puede esperar un aumento en los rendimientos de macarela, pero no así para macarela caballa ni anchoveta del norte.

INTRODUCTION

The purpose of this study is to describe the seasonal growth patterns of northern anchovy, *Engraulis mordax*, jack mackerel, *Trachurus symmetricus*, and Pacific mackerel, *Scomber japonicus* and to explore what these seasonal growth patterns suggest in terms of managing these fisheries.

Data for the study were provided by the California Department of Fish and Game (CDFG). Part of the data had been used previously to describe von Bertalanffy growth equations for northern anchovy (Spratt 1975), jack mackerel (Wine and Knaggs 1975), and Pacific mackerel (Knaggs and Parrish 1973). In our study, computer programs were developed to calculate and graph growth statistics for these three species.

At the time the market samples were taken, northern anchovy had a quota, a 5-inch size limit, and a closed season during summer. These regulations were established by the State of California. No such regulations existed for Pacific mackerel and jack mackerel. Currently, the Pacific Fisheries Management Council has established a quota, a 5-inch size limit, and a closed season for northern anchovy. The State of California has established a quota, a 10-inch size limit, and a closed season for Pacific mackerel. There are no such regulations for jack mackerel.

METHODS

Description of Data Base

Data for this study were obtained by the CDFG through their programs for sampling and aging commercial catches of northern anchovy, jack mackerel, and Pacific mackerel. Sampling procedures for north-

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[Manuscript received 13 February 1981.]

ern anchovy have been described by Collins (1969). However, the sampling procedures for the jack mackerel and Pacific mackerel data have not been published.

Data for northern anchovy were taken from landings in San Pedro and Monterey. The samples from the San Pedro landings consist of 58,347 fish and include the 1966/67 season and the 1968/69 through 1978/79 seasons. The samples from the Monterey landings consist of 4,902 fish and include seasons 1966/67 through 1969/70 and seasons 1971/72 through 1977/78. In southern California, at the time these samples were taken, the anchovy season opened in September and closed during June, July, and August. However, during the 1978/79 season, the anchovy season closed during July and August. In central California, the anchovy season opened in August and closed during June and July.

The data for jack mackerel and Pacific mackerel were taken from landings in San Pedro. The jack mackerel samples include seasons 1966/67 through 1970/71, and consist of 20,109 fish. The Pacific mackerel samples include seasons 1962/63 through 1973/74 and consist of 7,005 fish. During this period of time there was a severe decline in the population of Pacific mackerel. Landings were extemely limited, and few fish were sampled. Finally, in 1970, the State of California put a moratorium on Pacific mackerel landings, which continued until 1977.

The individual fish data include date of capture, length, weight (g), sex, maturity, annuli (rings), and year class. Jack mackerel and Pacific mackerel lengths were recorded as fork length (FL), and northern anchovy lengths were recorded as standard length (SL).

For the purpose of portraying the data, it is assumed that all fish are born in the same month of the year. The spawning season for both jack mackerel and Pacific mackerel is March through October, with the majority of spawning taking place April through August (Knaggs and Parrish 1973; Wine and Knaggs 1975). For this study, May will be considered the birth month of both jack mackerel and Pacific mackerel. Northern anchovy has a year round spawning season, with the majority of spawning taking place in February and March (Ahlstrom 1966). For northern anchovy, February will be considered the birth month.

In Pacific mackerel (Fitch 1951) and jack mackerel, rings are laid down on the otoliths near the time of the birthday and, thus, can be used as a measure of age. In northern anchovy, however, rings are laid down during the spring, with the majority laid down by June 1st (Collins and Spratt 1969). Therefore, in our study ages of northern anchovy were calculated based on rings and date of capture.

Data Analysis

A computer program was developed to calculate the number, the mean length, and the mean weight of fish by age and by month. The program also calculated maximum and minimum lengths, maximum and minimum weights, standard deviations of lengths, and standard deviation of weights by age and by month. Standard deviations were not calculated if there were less than ten observations. This program also produced graphs of age-length and age-weight relationships.

In order to more clearly describe the seasonal fluctuations in weight, the proportion of growth by month was calculated for each of the three species. The September mean weight was taken as a starting point because this is the month the fish are recruited to the fishery. The proportion was calculated by dividing each monthly mean weight of each age group by its corresponding September mean weight. This procedure resulted in an overlap of age groups. To avoid bias resulting from small numbers of fish at the older ages, the proportions were weighted by the number of fish. These calculations were made for younger fish (mostly immatures), for older fish (mostly adults), and for the total number of fish.

RESULTS

The relationships between age and length and between age and weight for northern anchovy, jack mackerel, and Pacific mackerel are shown in the following tables and figures. When expressed graphically the seasonal fluctuations in growth in weight, and to a lesser degree growth in length, are evident. Growth in weight has different seasonal patterns in the three species, and it also differs between anchovy landed in Monterey and San Pedro.

Seasonal Distribution of Catch by Age

The summaries of the number and mean length of fish by age and month for northern anchovy landed in San Pedro and Monterey show considerable differences in the age structure and the seasonality of the fisheries in the two regions. The data for northern anchovy sampled in San Pedro show that a very small percentage of the fish were less than one year old (3.2%); the bulk of the fish (83.8%) consisted of ages 1–3 (Table 1). One-year-old fish comprised 26% of the fish sampled; 33.8% of the fish were two years old, and 24% were three years old. The highest percentages of catch occurred in fall and early winter (October through January), with a small peak during the spring (April and May). Landings were low during the peak of the spawning season (February and March) and during the summer due to the closed season. A

TABLE 1
Number *(N)*, Mean Standard Length mm ($\bar{X}$), and Percentage of Fish by Age and Month for Northern Anchovy Sampled in San Pedro.

AGE		FEB	MAR	APR	MAY	JUN*	JUL	AUG	SEP	OCT	NOV	DEC	JAN	SUBTOTAL	% BY AGE
0	N	0	0	0	0	0	0	0	52	297	280	575	665	1869	.032
	$\bar{X}$	0	0	0	0	0	0	0	104	103	106	104	105		
1	N	684	1778	1842	1870	519	0	0	707	2059	1610	2016	2091	15176	.260
	$\bar{X}$	104	106	109	112	110	0	0	117	117	119	117	116		
2	N	1236	993	1526	1592	75	0	0	1585	3630	3514	3348	2234	19733	.338
	$\bar{X}$	113	116	117	118	119	0	0	121	123	124	124	122		
3	N	970	662	1700	1593	31	0	0	999	1743	2717	2187	1422	14024	.240
	$\bar{X}$	119	125	125	123	129	0	0	124	127	129	129	130		
4	N	409	554	1306	639	2	0	0	186	500	896	620	454	5566	.095
	$\bar{X}$	127	133	132	130	131	0	0	129	131	133	133	138		
5	N	110	348	591	180	0	0	0	25	63	125	88	95	1625	.028
	$\bar{X}$	136	139	138	138	0	0	0	133	136	136	138	144		
6	N	32	97	132	33	0	0	0	3	7	12	6	6	328	.006
	$\bar{X}$	141	146	144	145	0	0	0	144	136	142	142	156		
7	N	2	8	10	3	0	0	0	0	1	0	0	0	24	.0004
	$\bar{X}$	162	151	147	147	0	0	0	0	124	0	0	0		
8	N	0	1	1	0	0	0	0	0	0	0	0	0	2	.00003
	$\bar{X}$	0	147	172	0	0	0	0	0	0	0	0	0		
SUBTOTAL		3443	4441	7108	5910	627	0	0	3557	8300	9154	8840	6967	58347	
% BY MONTH		.059	.076	.122	.101	.011	0	0	.061	.142	.157	.152	.119		

*Represents only one season of data (1978/79)

small percentage (7.4%) of the anchovies sampled in Monterey were age group 0; most (83.7%) were age groups 1–4 (Table 2). The 1- to 4-year-old fish comprised 17.4%, 22.2%, 27.4%, and 16.7%, respectively, of the sampled catch. Peak landings occurred in the late summer and fall (August through November).

A comparison of the anchovy landings in the two areas shows that the fish landed in Monterey tend to be older than those landed in San Pedro. The median age in the Monterey samples was three, and the median age in the San Pedro samples was two. Peak landings in Monterey occurred earlier in the season and were more seasonally concentrated than those in San Pedro. In Monterey, 66% of the sampled catch was landed during the September-November period, whereas in San Pedro, 45.1% was landed during October-December.

The San Pedro landings of jack mackerel consisted primarily of young fish; 27.3% of the fish sampled were less than one year old, 49.5% were one-year-old fish, and 16.5% were two-year-old fish (Table 3). Only 6.6% of the fish were age three and older. The dominance of young fish in the catch is influenced by the fact that the bulk of the adult stock is not available

TABLE 2
Number *(N)*, Mean Standard Length mm ($\bar{X}$), and Percentage of Fish by Age and Month for Northern Anchovy Sampled in Monterey.

AGE		FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	SUBTOTAL	% BY AGE
0	N	0	0	0	0	0	0	6	45	46	252	11	4	364	.074
	$\bar{X}$	0	0	0	0	0	0	110	110	109	112	109	122		
1	N	1	28	19	11	0	0	175	228	242	112	15	21	852	.174
	$\bar{X}$	124	108	114	110	0	0	121	123	123	122	127	124		
2	N	7	46	52	14	0	0	122	275	295	152	65	60	1088	.222
	$\bar{X}$	126	120	125	126	0	0	131	133	131	133	132	132		
3	N	18	54	61	17	0	0	135	246	381	234	98	100	1344	.274
	$\bar{X}$	136	124	135	133	0	0	139	141	139	138	137	138		
4	N	22	55	47	1	0	0	71	141	188	153	72	67	817	.167
	$\bar{X}$	144	146	147	134	0	0	146	147	146	143	141	145		
5	N	23	14	29	2	0	0	28	78	62	63	24	22	345	.070
	$\bar{X}$	149	146	151	135	0	0	153	152	151	149	145	151		
6	N	7	9	20	0	0	0	4	24	6	6	5	1	82	.017
	$\bar{X}$	155	152	155	0	0	0	155	161	153	153	152	154		
7	N	0	0	5	0	0	0	0	3	0	2	0	0	10	.002
	$\bar{X}$	0	0	155	0	0	0	0	158	0	165	0	0		
SUBTOTAL		78	206	233	45	0	0	541	1040	1220	974	290	275	4902	
% BY MONTH		.016	.042	.048	.009	0	0	.110	.212	.249	.199	.059	.056		

TABLE 3
Number (*N*), Mean Fork Length mm ($\bar{X}$), and Percentage of Fish by Age and Month for Jack Mackerel Sampled in San Pedro.

AGE		MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR	APR	SUBTOTAL	% BY AGE
0	*N*	0	0	0	1	16	265	274	629	770	809	1507	1219	5490	.273
	$\bar{X}$	0	0	0	187	156	160	166	171	172	172	180	180		
1	*N*	1560	1868	904	1091	1175	1144	687	742	171	253	227	135	9957	.495
	$\bar{X}$	183	186	186	198	201	210	213	214	215	219	218	225		
2	*N*	589	506	351	200	168	427	264	243	100	134	199	144	3325	.165
	$\bar{X}$	227	230	228	233	237	238	235	235	241	242	243	249		
3	*N*	218	205	123	29	57	184	29	8	26	60	41	22	1002	.050
	$\bar{X}$	249	259	249	275	278	274	282	297	279	265	263	278		
4	*N*	43	61	28	3	33	48	10	5	18	17	14	7	287	.014
	$\bar{X}$	271	273	270	282	298	302	308	311	301	292	297	335		
5	*N*	3	4	5	1	1	8	4	2	2	12	1	0	43	.002
	$\bar{X}$	324	304	289	327	302	342	357	330	325	320	330	0		
6	*N*	1	0	0	0	0	0	1	0	0	1	1	0	4	.0002
	$\bar{X}$	345	0	0	0	0	0	362	0	0	317	325	0		
7'	*N*	0	0	1	0	0	0	0	0	0	0	0	0	1	.00005
	$\bar{X}$	0	0	335	0	0	0	0	0	0	0	0	0		
SUBTOTAL		2414	2644	1412	1325	1450	2076	1269	1629	1087	1286	1990	1527	20109	
% BY MONTH		.120	.131	.070	.066	.072	.103	.063	.081	.054	.064	.099	.076		

to the San Pedro purse seine fleet. Adult fish occur farther offshore and to the north of the fleet's fishing grounds (Blunt 1969). In addition, the absence of a size limit allows the take of small jack mackerel, which were apparently available to the fishery year round, since the data show no sharp peaks in monthly landings.

Pacific mackerel landings in San Pedro were dominated by age groups zero and one, 38.6% and 28.2% respectively (Table 4). The remaining percentage, 33.2%, was widely distributed among the other ages. In contrast to jack mackerel, older Pacific mackerel are available to the purse seine fishery as evidenced by the higher percentages of two- to six-year olds in the data. In addition, Fitch (1951) reported that the early fishery was dominated by two- to six-year olds. Catches of Pacific mackerel show strong seasonality, with a sharp peak in October/November. A second, minor peak, composed primarily of juveniles, occurred in May.

Growth in Length

The monthly distribution of lengths of northern anchovy in samples taken from the San Pedro and Mon-

TABLE 4
Number (*N*), Mean Fork Length mm ($\bar{X}$), and Percentage of Fish by Age and Month for Pacific Mackerel Sampled in San Pedro.

AGE		MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR	APR	SUBTOTAL	% BY AGE
0	*N*	0	0	0	0	150	720	579	369	329	268	139	152	2706	.386
	$\bar{X}$	0	0	0	0	201	211	226	231	245	237	230	237		
1	*N*	697	326	273	220	173	167	72	12	5	15	4	12	1976	.282
	$\bar{X}$	266	272	280	282	278	298	301	301	292	308	291	305		
2	*N*	64	35	107	55	45	138	57	16	1	10	8	42	578	.083
	$\bar{X}$	301	309	310	314	313	320	323	321	305	324	323	328		
3	*N*	33	41	62	29	62	148	84	45	4	19	12	5	544	.078
	$\bar{X}$	331	333	334	331	332	336	339	339	341	337	340	353		
4	*N*	60	27	51	36	23	105	39	27	0	6	7	3	384	.055
	$\bar{X}$	348	351	356	358	358	359	363	354	0	357	356	363		
5	*N*	68	13	23	29	11	182	61	66	4	8	8	2	475	.068
	$\bar{X}$	369	373	375	375	372	377	381	378	391	383	380	379		
6	*N*	24	2	14	5	8	115	32	52	18	9	0	0	279	.040
	$\bar{X}$	384	381	397	383	389	385	388	387	408	394	0	0		
7	*N*	1	0	7	2	1	17	1	9	5	2	0	0	45	.006
	$\bar{X}$	398	0	400	394	393	400	410	385	408	413	0	0		
8	*N*	1	0	3	0	1	9	0	0	0	1	0	0	15	.002
	$\bar{X}$	408	0	419	0	428	411	0	0	0	385	0	0		
9	*N*	0	0	1	0	0	2	0	0	0	0	0	0	3	.0004
	$\bar{X}$	0	0	408	0	0	416	0	0	0	0	0	0		
SUBTOTAL		948	444	541	376	474	1603	925	596	366	338	178	216	7005	
% BY MONTH		.135	.063	.077	.054	.068	.229	.132	.085	.052	.048	.025	.031		

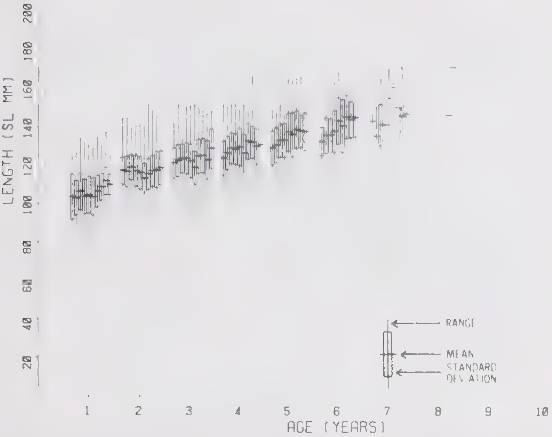

Figure 1. Monthly distribution (February-January) of the length of northern anchovy in samples taken from San Pedro (58,347 fish, 1966-78)

terey fisheries shows these fish have a slow growth rate, little seasonal fluctuations in mean standard length, and that anchovies landed in Monterey were larger than those landed in San Pedro. Young-of-the-year anchovies were recruited to the fishery in the fall (September-October). In San Pedro this occurred at a mean standard length of 103 mm (Figure 1, Table 1). By age four these fish had grown to a mean standard length of 130 mm. In Monterey, young-of-the-year anchovies were recruited to the fishery at a mean standard length of 109 mm and by age four had grown to a mean standard length of 146 mm (Figure 2, Table 2). At the time they entered the fishery, the anchovies landed in Monterey were 6 mm longer than the anchovies landed in San Pedro. This difference in standard length had increased to 16 mm by age four. The growth curves of anchovies in the two regions are almost linear and free of fluctuations.

The growth of anchovy described in this study differs from other published studies in that growth to age one is more rapid and growth after this age is slower. Clark and Phillips (1952) found one-year-old anchovies in central California to be 92 mm in standard length, and Spratt (1975) found one-year-old anchovies in southern California to be 92 mm in standard length. Using February as the birth month, we found one-year-old anchovies to be about 110 mm in central California and 104 mm in southern California. We also found that at age four anchovies in central California were 144 mm and anchovies in southern California were 127 mm. Clark and Phillips, however, found that anchovies in central California were 152 mm at age four, and Spratt found that anchovies in southern California were 135 mm at age four. The most likely explanation for the differences in growth rates among these studies is that anchovies have different growth rates in different years. Spratt's data cover the years 1966–72 and consist of 677 aged fish. Clark and Phillips' data cover the years 1946–51 and consist of 211 aged fish. Our study covers the years 1966–78 and consists of 58,347 aged fish for southern California and 4,902 aged fish for central California.

Young-of-the-year jack mackerel first entered the fishery during September-October at a mean fork length of 158 mm and reached 300 mm by the time they were four years old (Figure 3, Table 3). Fish that were three years and older tended to exhibit seasonal fluctuations in mean fork length; growth was more rapid in the spring and summer than in the winter. Growth in length of jack mackerel is well described by

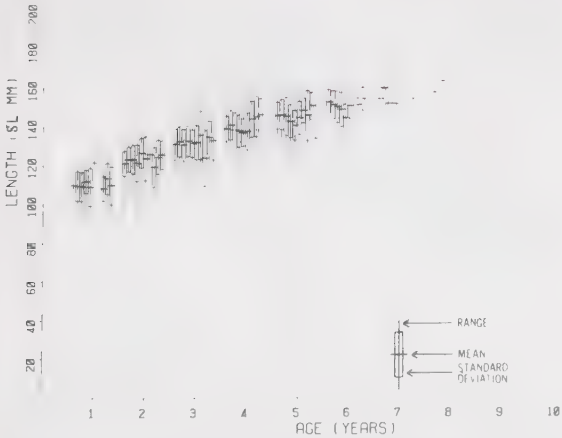

Figure 2. Monthly distribution (February-January) of the length of northern anchovy in samples taken from Monterey (4,902 fish, 1966-77).

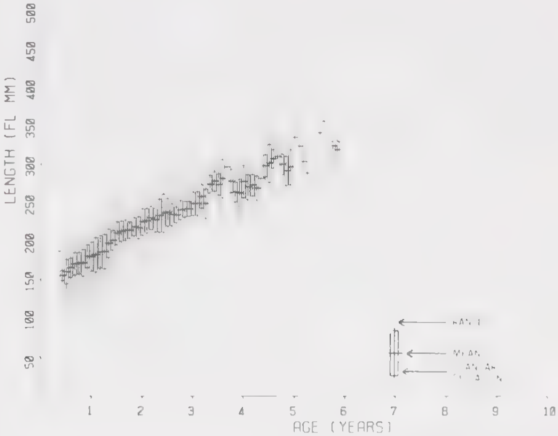

Figure 3. Monthly distribution (May-April) of the length of jack mackerel in samples taken from San Pedro (20,109 fish, 1966-70)

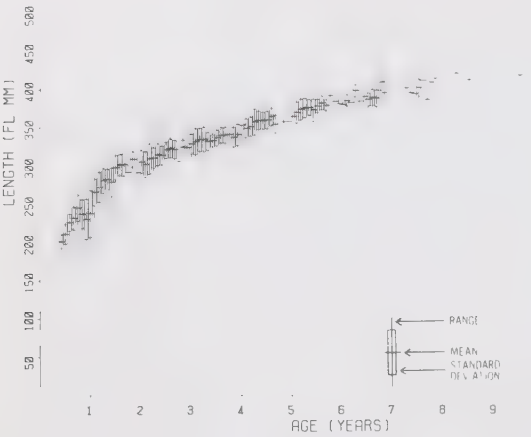

Figure 4. Monthly distribution (May-April) of the length of Pacific mackerel in samples taken from San Pedro (7,005 fish, 1962-73).

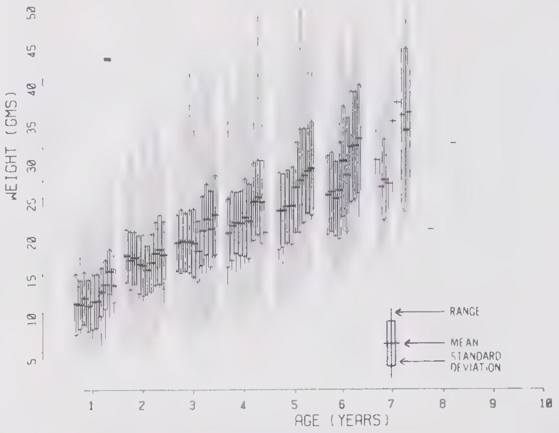

Figure 5. Monthly distribution (February-January) of the weight of northern anchovy in samples taken from San Pedro (58,296 fish, 1966-78).

a von Bertalanffy growth equation (Wine and Knaggs 1975).

Young-of-the-year Pacific mackerel are recruited to the fishery in September-October at a mean fork length of 206 mm (Figure 4, Table 4). These fish attained a length of 359 mm by the time they were four years old. Growth was particularly rapid during the spring and summer for one-year-old fish. Growth in length of Pacific mackerel appears to exhibit a close fit to a typical von Bertalanffy growth equation (Knaggs and Parrish, 1973).

Growth in length of jack mackerel and Pacific mackerel have several differences. Pacific mackerel initially have a faster rate of growth than jack mackerel. Although both enter the fishery in September (at about six months of age), Pacific mackerel have a mean fork length of 206 mm, whereas jack mackerel have a mean fork length of only 158 mm. Growth in Pacific mackerel is very rapid to about two years of age, then decreases somewhat in older fish. Jack mackerel, however, maintain a moderate, almost linear, growth rate. In addition, Pacific mackerel growth in length displays seasonality in one-year-old fish, whereas jack mackerel growth displays seasonality in fish three years and older.

Growth in Weight

The monthly distribution of northern anchovy weights in samples taken from the San Pedro fishery indicates that anchovies first entered the fishery at a mean weight of 11.1 g and by age four had increased to a mean weight of 23.2 g (Figure 5, Table 5).[1] In a period of four years, these fish had increased their weight by a factor of 2.1. Growth in weight shows a step-like fluctuation with no growth during the fall and winter months, followed by a spurt of growth beginning in late winter or early spring, which continues through early summer. Although there are no data over the summer months, it appears that younger fish (ages 1 and 2) increased in weight over these months, whereas older fish (ages 3+) lost weight over this period.

Northern anchovies were recruited to the Monterey fishery at a mean weight of 15.5 g (Figure 6, Table 6). By age four, they had increased to a mean weight of

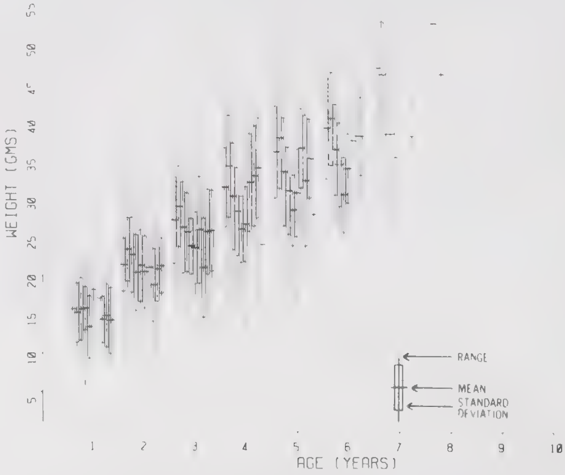

Figure 6. Monthly distribution (February-January) of the weight of northern anchovy in samples taken from Monterey (4,807 fish, 1966-77).

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[1] The total numbers of fish in Tables 1-4 are different from those in Tables 5-8 because some fish were not weighed

TABLE 5

Number *(N)*, Mean Weight g *($\bar{X}$)*, and Percentage of Fish by Age and Month for Northern Anchovy Sampled in San Pedro.

AGE		FEB	MAR	APR	MAY	JUN*	JUL	AUG	SEP	OCT	NOV	DEC	JAN	SUBTOTAL	% BY AGE
0	N	0	0	0	0	0	0	0	52	297	280	575	665	1869	.032
	$\bar{X}$	0	0	0	0	0	0	0	11.2	11.1	12.0	11.0	11.4		
1	N	684	1778	1842	1870	519	0	0	707	2059	1610	2016	2091	15176	.260
	$\bar{X}$	11.6	12.8	13.7	15.4	13.6	0	0	17.4	16.8	17.2	16.3	16.2		
2	N	1236	993	1517	1592	75	0	0	1585	3630	3514	3348	2234	19724	.338
	$\bar{X}$	15.6	16.5	17.7	18.3	17.5	0	0	19.1	19.3	19.2	19.3	19.1		
3	N	970	662	1683	1593	31	0	0	999	1743	2717	2187	1422	14007	.240
	$\bar{X}$	18.0	20.7	22.2	20.9	22.7	0	0	20.3	21.3	21.7	21.6	22.3		
4	N	409	554	1288	639	2	0	0	186	500	896	620	454	5548	.095
	$\bar{X}$	21.8	24.4	25.0	24.4	20.4	0	0	23.2	23.2	23.8	23.9	26.3		
5	N	110	348	586	180	0	0	0	25	63	125	88	95	1620	.028
	$\bar{X}$	27.1	27.8	28.4	28.7	0	0	0	25.2	25.7	24.8	25.8	29.6		
6	N	32	97	130	33	0	0	0	3	7	12	6	6	326	.006
	$\bar{X}$	27.8	31.5	31.6	32.5	0	0	0	29.7	26.3	27.2	26.7	34.7		
7	N	2	8	10	3	0	0	0	0	1	0	0	0	24	.0004
	$\bar{X}$	37.2	35.5	33.6	35.9	0	0	0	0	18.1	0	0	0		
8	N	0	1	1	0	0	0	0	0	0	0	0	0	2	.00003
	$\bar{X}$	0	31.9	58.2	0	0	0	0	0	0	0	0	0		
SUBTOTAL		3443	4441	7057	5910	627	0	0	3557	8300	9154	8840	6967	58296	
% BY MONTH		.059	.076	.121	.101	.011	0	0	.061	.142	.157	.152	.120		

*Represents only one season of data (1978/79)

35.7 g. These fish had increased their weight by a factor of 2.3 in four years. The growth of Monterey anchovies shows significant seasonal fluctuations. During the fall to mid-winter months, prior to the peak spawning period, there is a loss in mean weight, which is more pronounced in fish three years and older. Growth appears to be erratic from mid-winter to spring, and finally, from spring to fall, there is a marked spurt in growth.

There are differences in the growth in weight of anchovies in the two areas. At the time they entered the fishery, the anchovies landed in Monterey were 4.4 g heavier than those landed in San Pedro. This difference in weight had increased to 12.5 g by age four. In addition, the anchovies landed in Monterey have different seasonal fluctuations from those landed in San Pedro.

Jack mackerel increased their weight by a factor of 7.6 over a period of four years. Young-of-the-year fish entered the fishery at a mean weight of 42 g and reached a mean weight of 319 g by the time they were four years old (Figure 7, Table 7). Jack mackerel have a moderate rate of growth with little seasonality until age three. For fish three years and older, there is an

TABLE 6

Number *(N)*, Mean Weight g *($\bar{X}$)*, and Percentage of Fish by Age and Month for Northern Anchovy Sampled in Monterey.

AGE		FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	SUBTOTAL	% BY AGE
0	N	0	0	0	0	0	0	6	45	46	252	11	4	364	.076
	$\bar{X}$	0	0	0	0	0	0	15.7	15.3	15.7	15.8	13.4	18.2		
1	N	1	28	19	11	0	0	175	228	240	112	15	21	850	.177
	$\bar{X}$	17.1	14.3	14.9	14.2	0	0	21.4	23.4	22.8	20.4	21.3	20.5		
2	N	7	46	52	14	0	0	122	275	279	152	65	60	1072	.223
	$\bar{X}$	21.1	18.9	20.9	21.3	0	0	27.2	29.0	26.3	25.7	23.9	23.7		
3	N	18	54	61	17	0	0	135	246	339	234	98	100	1302	.271
	$\bar{X}$	26.0	21.1	25.7	25.9	0	0	31.5	34.3	30.3	28.4	26.1	26.8		
4	N	22	55	47	1	0	0	71	141	163	153	72	67	792	.165
	$\bar{X}$	32.1	33.0	34.0	24.1	0	0	36.1	37.9	33.6	31.1	28.6	30.8		
5	N	23	14	29	2	0	0	28	78	53	63	24	22	336	.070
	$\bar{X}$	36.6	32.4	35.3	28.1	0	0	39.2	40.4	36.4	34.5	30.6	34.0		
6	N	7	9	20	0	0	0	4	24	5	6	5	1	81	.017
	$\bar{X}$	37.6	38.2	38.1	0	0	0	47.0	46.2	38.4	38.5	35.5	37.9		
7	N	0	0	5	0	0	0	0	3	0	2	0	0	10	.002
	$\bar{X}$	0	0	38.2	0	0	0	0	52.8	0	46.2	0	0		
SUBTOTAL		78	206	233	45	0	0	541	1040	1125	974	290	275	4807	
% BY MONTH		.016	.043	.048	.009	0	0	.113	.216	.234	.203	.060	.057		

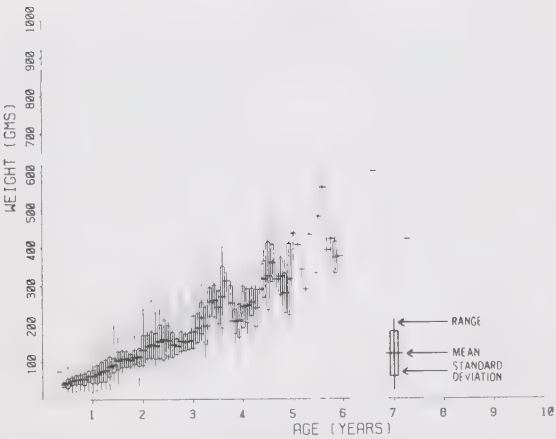

Figure 7. Monthly distribution (May-April) of the weight of jack mackerel in samples taken from San Pedro (20,068 fish, 1966-70).

increase in mean weight from late spring to late fall, followed by a loss in mean weight from winter to early spring.

Pacific mackerel entered the fishery at a mean weight of 102 g (Figure 8, Table 8). By age four, they had increased to a mean weight of 654 g, which represents an increase of 6.4 times the starting weight during this four-year period. Pacific mackerel, age groups 0-2, show a high growth rate and marked seasonal fluctuations. In these fish, a spurt of growth occurs from the spring to mid-winter months, followed by a small loss in weight during the mid-winter to spring months. For older fish (ages 3+), the number of fish per month was not sufficient to show a distinct seasonal pattern.

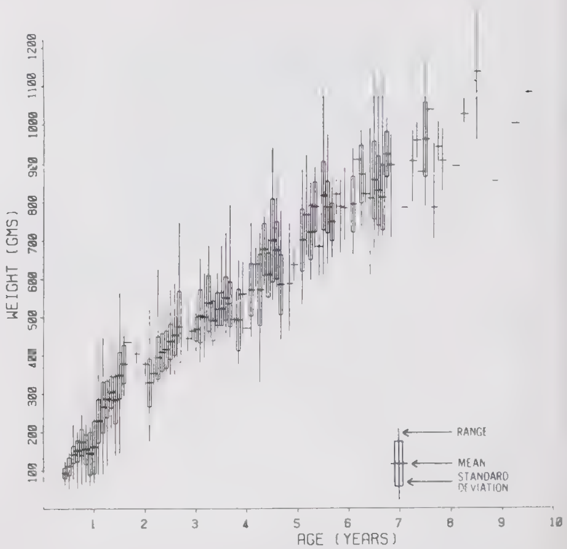

Figure 8. Monthly distribution (May-April) of the weight of Pacific mackerel in samples taken from San Pedro (6,054 fish, 1962-73).

There are several differences between the growth in weight of Pacific mackerel and jack mackerel. Pacific mackerel grow faster than jack mackerel, especially during their first few years. They enter into the fishery at a heavier weight (102 g) than jack mackerel (42 g) and seem to maintain this heavier weight overall. Pacific mackerel show seasonality in growth im-

TABLE 7

Number *(N)*, Mean Weight g ($\bar{X}$), and Percentage of Fish by Age and Month for Jack Mackerel Sampled in San Pedro.

AGE		MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR	APR	SUBTOTAL	% BY AGE
0	N	0	0	0	1	16	224	274	629	770	809	1507	1219	5449	.272
	$\bar{X}$	0	0	0	74	40	43	49	52	53	54	61	61		
1	N	1560	1868	904	1091	1175	1144	687	742	171	253	227	135	9957	.496
	$\bar{X}$	67	73	76	86	90	102	106	106	103	111	111	129		
2	N	589	506	351	200	168	427	264	243	100	134	199	144	3325	.166
	$\bar{X}$	139	143	140	152	157	154	143	139	152	150	153	177		
3	N	218	205	123	29	57	184	29	8	26	60	41	22	1002	.050
	$\bar{X}$	187	214	192	255	259	241	269	310	252	204	206	242		
4	N	43	61	28	3	33	48	10	5	18	17	14	7	287	.014
	$\bar{X}$	246	255	239	288	315	323	357	314	322	278	315	434		
5	N	3	4	5	1	1	8	4	2	2	12	1	0	43	.002
	$\bar{X}$	404	340	288	431	330	478	554	390	419	371	374	0		
6	N	1	0	0	0	0	0	1	0	0	1	1	0	4	.0002
	$\bar{X}$	494	0	0	0	0	0	596	0	0	385	402	0		
7	N	0	0	1	0	0	0	0	0	0	0	0	0	1	.00005
	$\bar{X}$	0	0	418	0	0	0	0	0	0	0	0	0		
SUBTOTAL		2414	2644	1412	1325	1450	2035	1269	1629	1087	1286	1990	1527	20068	
% BY MONTH		.120	.132	.070	.066	.072	.101	.063	.081	.054	.064	.099	.076		

TABLE 8

Number *(N)*, Mean Weight g *($\bar{X}$)*, and Percentage of Fish by Age and Month for Pacific Mackerel Sampled in San Pedro.

AGE		MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR	APR	SUBTOTAL	% BY AGE
0	N	0	0	0	0	150	720	576	369	329	260	138	150	2692	.445
	$\bar{X}$	0	0	0	0	93	111	141	151	174	155	144	161		
1	N	685	305	231	199	153	115	51	1	0	6	0	5	1751	.289
	$\bar{X}$	229	265	286	304	284	348	377	434	0	404	0	377		
2	N	41	9	78	32	32	110	41	11	0	6	6	24	390	.064
	$\bar{X}$	329	353	394	408	415	436	452	474	0	444	463	468		
3	N	17	8	20	13	50	114	63	39	4	15	9	1	353	.058
	$\bar{X}$	502	499	536	490	521	521	549	534	493	492	559	470		
4	N	47	6	12	13	11	38	22	23	0	4	7	0	183	.030
	$\bar{X}$	570	637	570	675	609	698	672	583	0	585	634	0		
5	N	64	6	13	21	8	131	52	66	4	4	8	0	377	.062
	$\bar{X}$	698	763	718	784	681	813	783	745	817	785	781	0		
6	N	23	1	13	5	7	87	32	52	18	9	0	0	247	.041
	$\bar{X}$	791	907	869	818	807	854	827	809	922	893	0	0		
7	N	1	0	7	2	1	16	1	9	5	2	0	0	44	.007
	$\bar{X}$	782	0	903	957	875	959	1036	782	939	904	0	0		
8	N	1	0	3	0	1	8	0	0	0	1	0	0	14	.002
	$\bar{X}$	889	0	1023	0	1109	1133	0	0	0	849	0	0		
9	N	0	0	1	0	0	2	0	0	0	0	0	0	3	.0005
	$\bar{X}$	0	0	998	0	0	1080	0	0	0	0	0	0		
SUBTOTAL		879	335	378	285	413	1341	838	570	360	307	168	180	6054	
% BY MONTH		.145	.055	.062	.047	.068	.222	.138	.094	.059	.051	.028	.030		

mediately after entering the fishery, whereas jack mackerel show little seasonality until age three.

Proportion of Growth in Weight by Month

Growth in weight of northern anchovy is highly seasonal, and the pattern of growth differs between the fish landed at San Pedro and those landed at Monterey. The San Pedro anchovies achieved nearly all of their annual increase in weight during the period of February to May (Figure 9A, Table 9). However, the pattern of growth is somewhat different in young and old fish. Younger fish, age groups 0-1, showed a slight decrease in weight from September to February, while older fish, ages 2+, showed a small weight gain. The young fish grew rapidly from February to May and essentially maintained their weight until September, while older fish grew rapidly from February to April, but lost about half of this increase in weight by September. At the end of a year, the San Pedro anchovies had an 18% increase in weight. However, the younger fish exhibited much more growth than the older fish (24% versus 8%). In the Monterey fishery, anchovies lost weight from September to May, and gained weight May to September (Figure 9B, Table 9). The younger fish, age groups 0–1, showed a similar seasonal pattern, but they had a more rapid growth rate from May to September. (Notice that there were few young fish sampled from December to May.) The older fish, ages 2+, showed a marked weight loss (23%) from September to De-

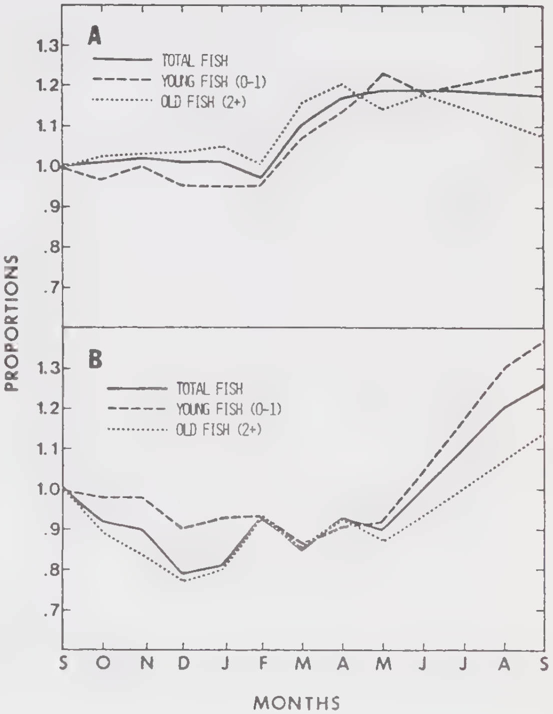

Figure 9. Proportion of growth in weight by month for (A) northern anchovy sampled in San Pedro (no data for July and August) and (B) northern anchovy sampled in Monterey (no data for June and July).

TABLE 9

Seasonal Variation in the Weight* of Northern Anchovy, Jack Mackerel, and Pacific Mackerel.

	SEP	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP
San Pedro anchovy													
Young (0-1)	1.00	.97	1.00	.95	.95	.95	1.07	1.13	1.23	1.19			1.24
Old (2+)	1.00	1.02	1.03	1.03	1.05	1.00	1.16	1.20	1.14	1.18			1.08
Total	1.00	1.01	1.02	1.01	1.01	.97	1.10	1.17	1.19	1.19			1.18
Monterey anchovy													
Young (0-1)	1.00	.98	.98	.90	.93	.93	.86	.91	.92			1.30	1.37
Old (2+)	1.00	.89	.84	.77	.80	.94	.85	.93	.87			1.07	1.14
Total	1.00	.92	.90	.79	.81	.93	.85	.93	.90			1.20	1.26
Jack mackerel													
Young (0-2)	1.00	1.09	1.13	1.18	1.26	1.28	1.43	1.48	1.60	1.74	1.75	2.07	2.16
Old (3+)	1.00	.97	1.12	1.13	1.01	.85	.85	1.04	.98	.99	.92	1.18	1.21
Total	1.00	1.08	1.13	1.18	1.25	1.25	1.42	1.47	1.59	1.72	1.73	2.07	2.14
Pacific mackerel													
Young (0-1)	1.00	1.20	1.50	1.62	1.86	1.66	1.53	1.72	2.39	2.80	2.65	3.02	2.78
Old (2+)	1.00	1.09	1.09	1.03	1.14	1.02	1.09	1.12	1.14	1.23	1.20	1.25	1.22
Total	1.00	1.16	1.40	1.42	1.81	1.58	1.47	1.63	2.17	2.70	2.39	2.68	2.32

*Expressed as a proportion of the September mean weight.

cember, much of which was regained between December and February; little change in weight occurred during the February to May period. All of their net annual increase in weight occurred from May to the following September. At the end of a year, the anchovies landed in Monterey showed a 26% increase in weight; young fish showed a 37% increase while the older fish showed a 14% increase. A comparison of the growth patterns of anchovies in the two regions shows that San Pedro anchovies increased in net weight from February to May and the Monterey anchovies increased in net weight from May to September. Other than the increase in weight that occurred from February to May, the anchovies in the San Pedro fishery showed little variation in weight. In the Monterey fishery, however, anchovies showed a loss in weight from September to May. At the end of a year, young anchovies at Monterey showed a 54% greater increase in weight than young anchovies at San Pedro; older anchovies at Monterey showed a 75% greater increase than those at San Pedro.

As previously mentioned, there are considerable differences in the growth patterns of jack and Pacific mackerel; growth is also different in the young and older individuals of both species. The data on these two species are heavily biased toward young fish, and therefore, the growth pattern of combined young and old fish is essentially the same as that for young fish. The ages chosen to represent young and old fish in jack mackerel differ from those chosen in the other two species. The natural break between the steady growth rate of young jack mackerel and the seasonal growth of older jack mackerel occurs between the ages of two and three (Figure 7).

The growth pattern for young jack mackerel, age groups 0–2, shows a steady increase in weight all year long (Figure 10A, Table 9). The older fish, ages 3+, showed an increase in weight from September to December, followed by a loss in weight from December

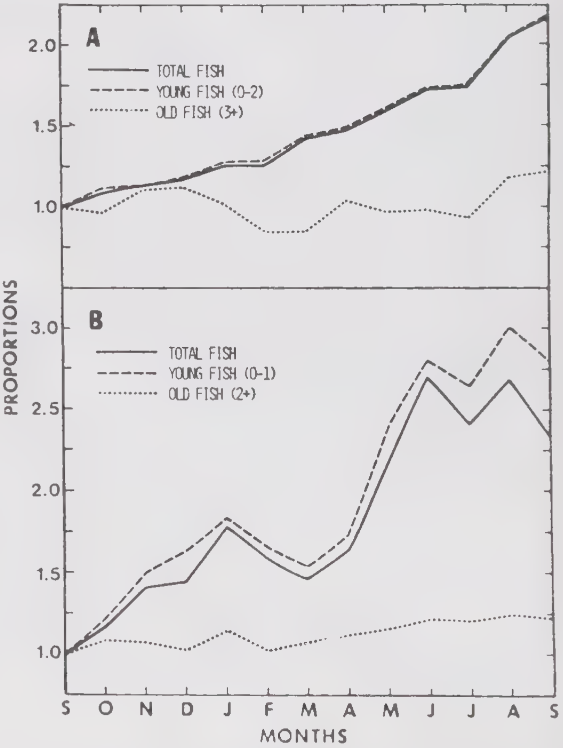

Figure 10. Proportion of growth in weight by month for (A) jack mackerel sampled in San Pedro and (B) Pacific mackerel sampled in San Pedro.

to February/March. There is little net growth from February to July. Essentially all of the net increase in weight occurs from July to September. At the end of a year, the older fish showed a 21% net increase in weight, while the younger fish showed a 116% net increase in weight.

The growth pattern for young Pacific mackerel, age groups 0-1, shows tremendous growth all year long except for a small loss in weight from January to March (Figure 10B, Table 9). The older fish, ages 2+, showed a general increase in weight from September to January. Then there is a loss in weight during late winter followed by a period of steady growth from spring to the following September. Young Pacific mackerel showed an annual net increase in weight of 178%, while the older fish showed an annual net increase of 22%. The seasonal growth patterns of jack mackerel and Pacific mackerel show that both young and old Pacific mackerel and older jack mackerel have a loss in weight from approximately winter to spring. Both young jack mackerel and young Pacific mackerel grow very quickly, but the annual growth of young Pacific mackerel is 53% greater than young jack mackerel. Older Pacific mackerel showed a 5% greater annual increase in weight than older jack mackerel.

DISCUSSION

The data presented for the seasonal distributions of lengths show that growth in length is relatively free of seasonal variation in the California stocks of northern anchovy, jack mackerel, and Pacific mackerel. The exceptions to this occur in jack mackerel older than three years, and in young-of-the-year and yearling Pacific mackerel, where growth in length is more rapid in the spring and summer than in the winter. Other than these minor exceptions, growth in length of these species is adequately described by von Bertalanffy growth equations. The situation for growth in weight is another matter; seasonal variation in growth is very large and can vary with age and geographical area.

Anchovies in California gain nearly all of their annual net increase in weight during a short period of the year. In southern California, growth begins in February and extends until April or May. Young fish essentially maintain this same weight until the next February, while older fish lose more than half of the weight gained by September. Anchovies in central California achieve their annual net increase in weight three to four months later than those in southern California. The net increase in weight starts in the period from May to July and extends to September. During the next winter, much or all of this increase will be lost, depending on the age of the fish. It should be noted that anchovies landed in San Pedro are from the central stock, whereas those landed in Monterey are probably from both the central and northern stocks (Vrooman et al. 1981).

Jack mackerel less than three years of age show little seasonality in growth in weight, whereas jack mackerel older than three years and post-recruit Pacific mackerel have weight losses during the late winter or early spring and weight gains during the rest of the year. The most rapid increase in weight in Pacific mackerel occurs when they are one year old, during the spring and summer. In jack mackerel the most rapid increase in weight occurs when they are three years old, also during the spring and summer. In jack mackerel this period marks the transition from a steady increase in weight to seasonal increases. In both Pacific and jack mackerel this rapid increase in weight occurs when the fish are about 250 mm in fork length. It appears that at this length there is a change in some life history feature, possibly in feeding habits, which results in a rapid increase in weight.

One of the major uses of data on the growth of commercially important fishes is the application of this information to fisheries management. The principal relationship of interest is that between the age and the total weight of an individual cohort. If fishing effort is large, it is theoretically possible to maximize yields by protecting the cohort from harvesting as long as the total weight of the cohort is increasing. The more quickly the cohort is gaining weight the more likely are there to be economic benefits from protection of younger fish. The relative advantage or disadvantage of a size limit can be readily observed by comparing the observed growth in weight with the growth that would be necessary to maintain a constant cohort weight.

The annual mortality rate for nothern anchovy is about 66% per year ($Z = 1.1$, MacCall 1974). Without a fishery the number of fish in a cohort would be expected to decline annually by two-thirds. In order to maintain a constant cohort weight, anchovies would have to triple their weight each year; as shown earlier, anchovies do not triple their weight even in four years. The largest annual anchovy growth rate observed in our study was the 55% increase in weight achieved by age group zero fish at San Pedro. This indicates that the growth rate of post-recruit anchovies is not sufficient to maintain the cohort biomass. If younger fish were not protected by regulations, the age composition of the catch would be expected to approximate that of the population. That is, the numbers of fish in each succeeding age group would decline by two-thirds or more (depending on the size of the fishery). The age composition of northern anchovy in the San Pedro fishery does not approach this decay rate until the transition from age three to four. The observed proportions of age groups zero to four (0.03, 0.26, 0.33, 0.24, 0.09) indicate that the present regulations provide almost total protection for young-of-the-year fish, considerable protection for yearlings, and some protection for two-year-old-fish.

The data presented in this study suggest that, in anchovy, maximum cohort weight occurs before recruitment to the fishery. Therefore, the size limit provides protection to cohorts for at least two years beyond the time they achieve maximum biomass. Small pelagic fishes are subject to recruitment overfishing (Cushing 1975), and in the absence of any other controls a size limit could be a desirable regulation for preventing this. However, when protection against recruitment overfishing is provided by an annual quota based on the spawning stock size, as in the case with the California anchovy fishery, the principal effect of a size limit is to increase the total effort and costs necessary to harvest the quota.

The use of growth information as a tool for fisheries management of jack mackerel is affected by the lack of good estimates for their natural mortality rate. It is also influenced by the fact that jack mackerel are increasingly unavailable to the fishery after age two. If, for want of a better estimate, it is assumed that young jack mackerel (age 0-2) have a mortality rate equal to that of Pacific mackeral ($M = 0.5$, Parrish and MacCall 1978), in the absence of a fishery, about 40% of the fish will die each year. To maintain a constant cohort weight, young jack mackerel would have to gain about 67% of their weight each year. In their first year in the fishery, age group zero in September to age group one in September, jack mackerel increased in weight by about 125%. In their second and third years in the fishery the increase was about 74% and 64%. This growth rate implies that it might be possible to increase the yields of jack mackerel by protecting fish less than one year old. However, before it could be determined if a size limit would be economically beneficial, it would be necessary to have a good estimate of natural mortality. It would also be necessary to evaluate whether the probability of capturing jack mackerel, before they become unavailable to the purse-seine fishery, is high enough to warrant protection of young fish.

Pacific mackerel have the fastest growth of the three species discussed. They more than triple their weight during their first year in the fishery. In their second and third years in the fishery they increase their weight by 46% and 26%. The annual mortality rate of Pacific mackerel is about 40% per year ($M = 0.5$, Parrish and MacCall 1978). Maximum cohort weight occurs about two years after recruitment. However, after the fish have been in the fishery for one year, the cohort biomass does not increase greatly (i.e. growth at 46% and mortality at 40%). Growth is particularly quick during the yearling spring and summer. A size limit that would protect Pacific mackerel until they have completed this growth spurt would be expected to increase yields.

The growth patterns of northern anchovy, jack mackerel, and Pacific mackerel described in this study suggest different management strategies. Maximum cohort biomass occurs before the anchovy enter the purse-seine fishery. Therefore, growth overfishing is unlikely to occur in this species even without a size limit or mesh-size limitation. Pacific mackerel are subject to growth overfishing, and the question is as yet unresolved for jack mackerel.

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Anchored Fish Aggregating Devices in Hawaiian Waters

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ABSTRACT—Fish aggregating devices (FAD's) made of 55-gallon oil drums and wooden rafts were moored in Hawaiian waters off the islands of Oahu, Lanai, and Hawaii from May 1977 through July 1979. The FAD's successfully attracted numerous pelagic fishes, including large schools of skipjack and small yellowfin tunas. Commercial tuna pole-and-line boats benefited greatly by taking large catches of tunas from around the FAD's. Fishing around the FAD's resulted in reduced fuel and baitfish expenses. Trolling boats also benefited as they experienced a reduction in the number of zero-catch days. The success of the FAD experiment encouraged the State of Hawaii to implement its own FAD system involving 26 fish aggregating devices around seven major islands.

Introduction

Tunas have long been known to aggregate around floating objects such as logs, masses of drifting seaweed, debris, and other flotsam. Both Japanese and American fishermen have utilized this knowledge and routinely seek such objects while fishing for skipjack tuna, *Katsuwonus pelamis*, and yellowfin tuna, *Thunnus albacares*, in the eastern and western Pacific (Uda, 1933; Kimura, 1954; McNeely, 1961; Inoue et al., 1963, 1968).

In recent years, the Japanese began seining for skipjack and small yellowfin tunas in the western equatorial Pacific. The Pacific Tuna Development Foundation (PTDF) also began similar operations in the western Pacific with chartered American seiners (PTDF, 1979). In both operations the success of seining for tunas depended largely upon schools associated with drifting logs. The ratio of successful sets in the PTDF operations was well over 4:1 in favor of sets made around drifting logs as compared with sets made on schools independent of logs.

While the value of drifting logs to successful seining has been well demonstrated by these questions, such logs, which abound in the western equatorial Pacific, especially in waters north of Papua New Guinea, are only seldom found around islands in the central Pacific. Moreover, whenever an occasional log is encountered in the latter areas, it is available to the local fishermen only for a short time before it drifts off beyond the range of their boats. Thus, to benefit from this type of fishing in areas where drifting logs are scarce, it may be necessary for man to turn to anchored devices.

This has been done in the Philippines in recent years where purse seining for tunas around large bamboo rafts (7 × 36 feet) anchored in very deep waters (2,000-3,000 fathoms) has developed into a sizable tuna fishery (Matsumoto[1]). The anchored rafts, numbering in the hundreds and spaced 4-8 miles apart, have successfully attracted large quantities of tunas and enabled the seiners to operate continuously for 6 months or more at a time. The success of this fishery has been mainly due to the availability of vast areas of protected waters in the Philippines where the seas are exceptionally calm.

The Honolulu Laboratory of the National Marine Fisheries Service (NMFS) Southwest Fisheries Center and the PTDF embarked on a joint project to test anchored fish aggregating devices in Hawaiian waters in May 1977. The project was funded largely by PTDF with additional support from NMFS. This report covers the procedures and results of the project.

Objectives

The primary objectives of the project were to: 1) Develop and test anchored fish aggregating devices (hereafter called buoys) in open ocean areas and 2) determine their effect upon the skipjack tuna pole-and-line fishery in Hawaii. Secondary objectives were to determine the effects of buoy placement relative to distance from land, depth, and bottom topography.

Procedure

Buoy Construction

Two types of buoys were used in the experiment. The first type (Fig. 1, 2) consisted of a buoy made of two 55-gallon steel oil drums filled with polyurethane foam and held together in a frame of 3- × 3-inch angle iron. The frame was extended below to form V's at the front and rear and wooden slats were bolted to the V sections to form a haven for small fish. This also provided additional stability to the buoy. A pyramid made of angle iron and plywood

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[1] Matsumoto, W. M. Seine fishing around payaos in the Philippines. Honolulu Laboratory, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Honolulu, HI 96812. Manuscr. in prep.

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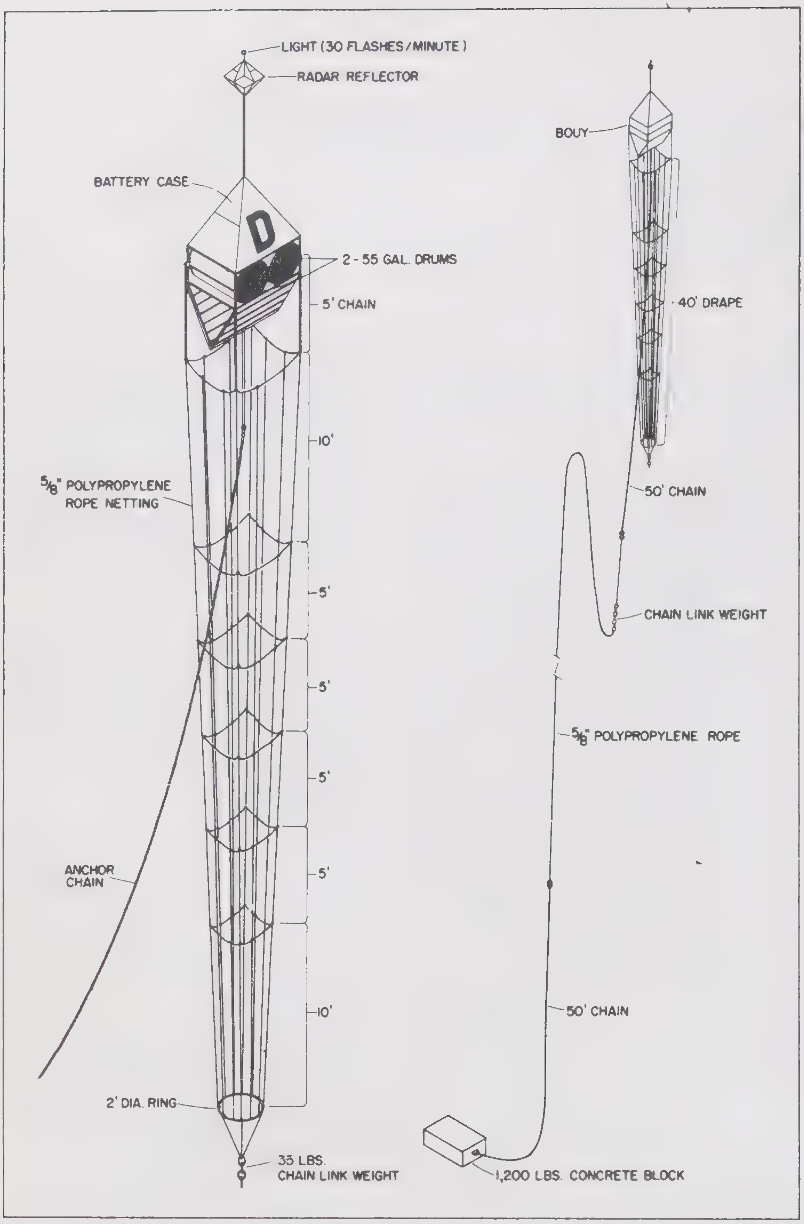

Figure 1.—Fish aggregating device, buoy type.

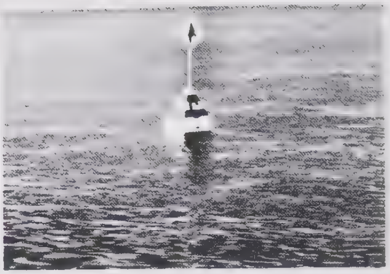

Figure 2.—Fish aggregating device in place off Oahu, Hawaii.

was welded over the drums and a radar reflector and a navigational warning light were mounted above the pyramid. Details of the buoy and radar reflector are shown in Figures 3 and 4.

A battery compartment was built into the upper half of the pyramid, which was painted in alternate orange and white horizontal bands and marked A, B, C, etc. The light, which was equipped with a photosensor and flashed 32 times per minute, was visible at 0.75 mile. It was energized by three 6-V lantern batteries encased in a length of 3-inch polyvinyl chloride (PVC) pipe. The battery pack provided energy for up to 5 months.

Initially, a 1 × 3 × 30-foot raft made of 1½-inch PVC pipes bolted onto metal frames with floats at both ends was tethered to the buoy. Six to eight coconut palm fronds attached to a 50-foot cable were suspended from the end of the raft. The palm fronds were soon found to be too fragile to withstand the prevailing wave action, and the raft itself was prone to excessive damage because it collided with the buoy in rough seas. Consequently, both raft and fronds were removed from the buoy and a drape made of polypropylene rope was suspended directly from the buoy (Fig. 1).

The second type was a raft (Fig. 5), 4 × 12 feet, made of 2- × 6-inch wooden planks on top and bottom and bolted to four 4- × 4-inch crosspieces. The space between the top and bottom layers of planks was filled with polyurethane foam. A superstructure identical with that used on the buoy was mounted on the raft and a drape, made of 1-inch mesh nylon netting, was hung from the rear third of the raft. These rafts were used only off Kona, Hawaii.

Anchor and Mooring Method

The anchor consisted of a 1,200-pound block of concrete, reinforced with steel bars, and fitted with a ¾-inch galvanized eyebolt at one end.

The anchor line consisted of 50-foot

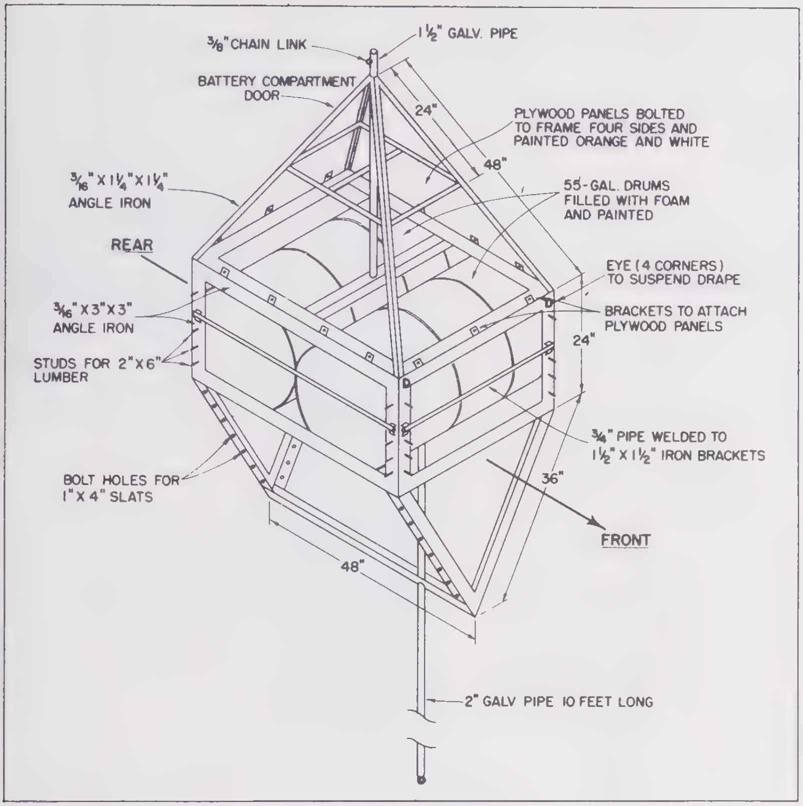
⅜" CHAIN LINK
1½" GALV. PIPE
BATTERY COMPARTMENT DOOR
24"
PLYWOOD PANELS BOLTED TO FRAME FOUR SIDES AND PAINTED ORANGE AND WHITE
48"
3/16" X 1¼" X 1¼" ANGLE IRON
55-GAL. DRUMS FILLED WITH FOAM AND PAINTED
REAR
EYE (4 CORNERS) TO SUSPEND DRAPE
3/16" X 3" X 3" ANGLE IRON
BRACKETS TO ATTACH PLYWOOD PANELS
24"
STUDS FOR 2" X 6" LUMBER
¾" PIPE WELDED TO 1½" X 1½" IRON BRACKETS
BOLT HOLES FOR 1" X 4" SLATS
36"
FRONT
48"
2" GALV PIPE 10 FEET LONG

Figure 3.—Details of two-drum buoys.

lengths of ½-inch galvanized chain at the top and bottom and a main section of ⅝-inch twisted polypropylene rope. The scope or ratio of anchor line to depth was between 1.65:1 and 1.80:1. Such a large scope, together with the positive buoyancy of the polypropylene rope, caused large sections of anchor line to float at the surface periodically during changes in the tidal current and thereby posed a hazard to navigation. To correct this, a chain link weight was added to the upper one-fourth to one-third of the anchor line to keep the excess line submerged at all times. The position and size of the weight varied from one buoy to the next, depending upon the length of the anchor line and the depth of the anchoring site. The weight was linked into the line to prevent it from chafing the anchor line.

The simplest method was used in mooring the buoys. The buoy was first set on the water at the selected site, the anchor line was payed out as the vessel moved slowly in a circular path around the buoy, and the anchor was released in a free fall to the bottom.

Location of Buoys

Four buoys were initially moored off Oahu and Lanai (Fig. 6) on 9 and 10 May 1977. Buoy A was placed 16 miles south-southwest of Kewalo Basin (lat. 12°04′N, long. 158°00.4′W), Oahu, at a depth of 308 fathoms; buoy B was placed 18 miles southeast of Kewalo Basin and 1 mile off Penguin Bank (lat. 21°00.5′N, long. 157°43.7′W) at a depth of 242 fathoms; buoy C was moored 27 miles south-southeast of Kewalo Basin and 1.1 miles off the tip of Penguin Bank (lat. 20°51′N, long. 157°45′W) at a depth of 246 fathoms; and buoy D was moored 10.5 miles southwest of Lanai (lat. 19°20′N, long. 157°10′W) at a depth of 345 fathoms. Buoys A and D were situated within 2 miles of the 500- to 1,000-fathom slope, whereas buoys B and C were 14 and 6 miles, respectively, from the slope.

The first three buoy sites were fully exposed to the northeast trades, which predominated in all seasons, and to occasional south winds, often accompanied by storms. The buoys were thus buffeted by winds from 15 to 25 knots, often approaching gale force. The seas were generally from 4 to 12 feet but exceeded 20 feet during storms. Site D was relatively calmer, with seas generally ranging from 2 to 4 feet. During stormy periods, however, the seas ranged as high as 10 feet.

Subsequently, on 22 March 1978, two raft-type devices were moored off Kona, Hawaii, in relatively calm waters. The first, F, was placed 4.5 miles west of Kaiwi Point at a depth of 1,250 fathoms and the second, G, was placed 6 miles offshore and 8 miles north-northwest of Keahole Point at a depth of 220 fathoms. The latter was situated 3.5 miles shoreward from the 1,000-fathom slope. Both of these sites were in proven fishing areas for tunas and billfishes.

Monitoring Buoys and Catches

Monitoring and maintenance of the buoys off Oahu and Lanai were scheduled on a monthly basis, with additional visits at the height of the skipjack tuna fishing season. All visits could not be made as planned, however, due to prolonged periods of rough sea conditions.

On all monitoring trips, troll fishing was done at each buoy site and on runs between buoys. Sightings of bird flocks, fish schools, and scattered birds were recorded and the areas immediately around the buoys were scanned with a depth recorder to detect subsurface fish schools.

Fish catch data from commercial tuna pole-and-line boats visiting the buoys were obtained through catch forms supplied to each boat and from interviews with boat operators. Catch data from commercial and recreational trolling boats were obtained from interviews once or twice each week and were limited to boats based at Kewalo Basin,

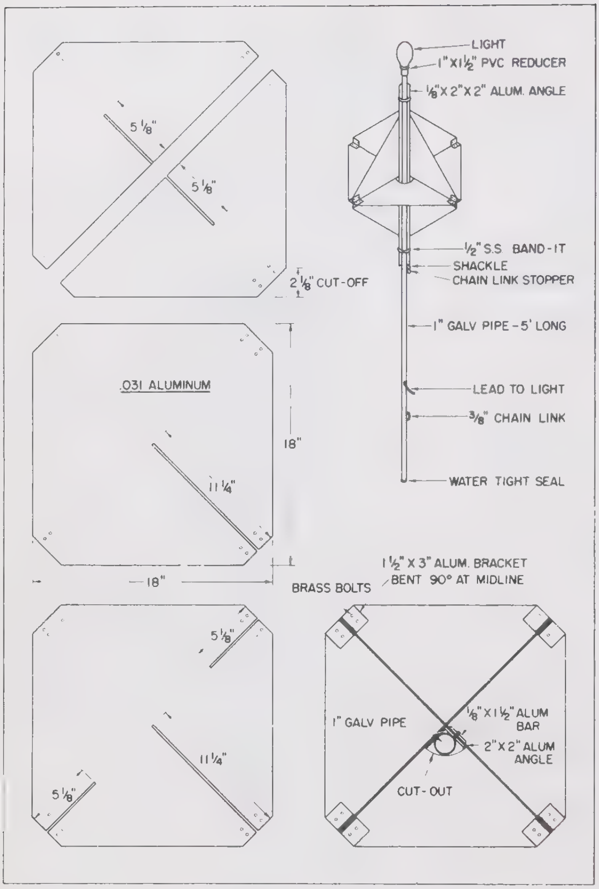

Figure 4.—Details of radar reflector.

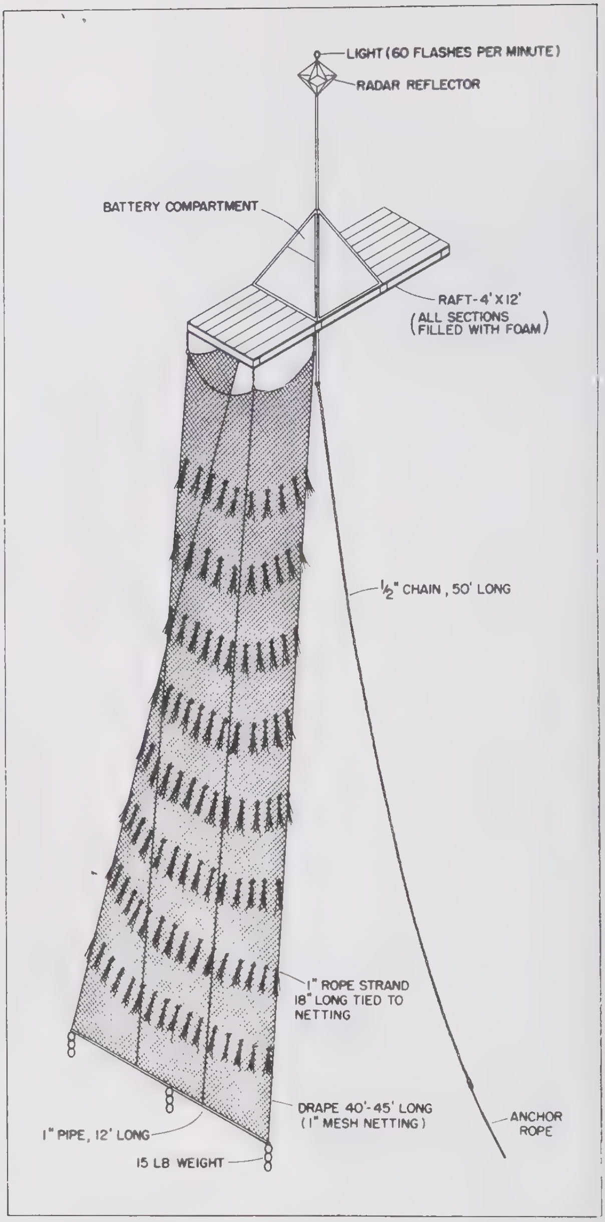
LIGHT (60 FLASHES PER MINUTE)
RADAR REFLECTOR
BATTERY COMPARTMENT
RAFT-4' X 12'
(ALL SECTIONS FILLED WITH FOAM)
½" CHAIN, 50' LONG
1" ROPE STRAND 18" LONG TIED TO NETTING
DRAPE 40'-45' LONG (1" MESH NETTING)
ANCHOR ROPE
1" PIPE, 12' LONG
15 LB WEIGHT

Figure 5.—Fish aggregating device, raft type.

since it was not possible to monitor the numerous trailer boats launched from scattered points on the island. Fish catch forms also were distributed to boats fishing out of Kona and Maui. Underwater observations were made at buoys D and F, both located in calm water.

Results

Buoy Performance

The buoys performed as expected in attracting and holding marketable fish species. The dolphin, *Coryphaena hippurus*, and wahoo, *Acanthocybium solanderi*, were among the first to be caught by trolling around the buoys. These fish appeared from 1 to 3 weeks after the buoys had been anchored. Both species generally appeared in small numbers but sizable catches of 10-20 dolphin were reported on 14 occasions and 20-30 fish on 4 occasions. The two largest single-day catches of this species were 32 and 41 fish.

Schools of tunas, small yellowfin, skipjack, and kawakawa, *Euthynnus affinis*, generally appeared from 2 to 5 weeks after the buoys had been deployed. The early arrivals were small fish weighing from 1 to 4 pounds. These were joined later by larger fish as the tuna aggregations increased around the buoys. Other fish of the families Carangidae, Balistidae, and Kyphosidae often appeared well before the tunas.

As the aggregations of fish built up around the buoys, so did the number of fishing boats. These included commercial bait boats, chartered (sport fishing) and commercial trollers, and trailer boats of assorted sizes. Buoy A attracted as many as 30 boats on a given day, all fishing simultaneously around the buoy and up to a distance of 3 miles. In the calmer waters off Kona, F and G buoys attracted 50 or more boats on a given day.

Buoy losses were experienced at all sites. The four buoys (A-D), initially deployed on 9 and 10 May 1977, broke free in July after 7-10 weeks because of incompatible fittings used in the anchor line. Subsequently, two more buoys were lost at sites A and B and one more each at sites C and D from other causes. At site A, the second buoy was lost after 16.5 months as a result of a storm and the third buoy was lost after 4.5 months, due to cable grip slippage. On this buoy, 100 feet of ⅜-inch cable, secured by three safety cable grips at each end, was used at the top of the anchor line, instead of the usual length of chain. At site B, the second buoy was lost after 3 months as a result of line chafing. The buoy was inadvertently anchored too close to Penguin Bank, and the anchor rope failed to clear the top of the ledge as the buoy swung over the bank during tidal changes. The third buoy was lost after 16.75 months when a shackle pin was lost. At site C, the second buoy was lost after 19.75 months due to undetermined causes, and at site D, the second buoy was lost after 16.5 months after it had been dragged by currents to a shallow ledge where the anchor rope eventually chafed on the bottom. Despite these losses, the buoys at all sites remained in position long enough to demonstrate their effectiveness in attracting and holding fish schools.

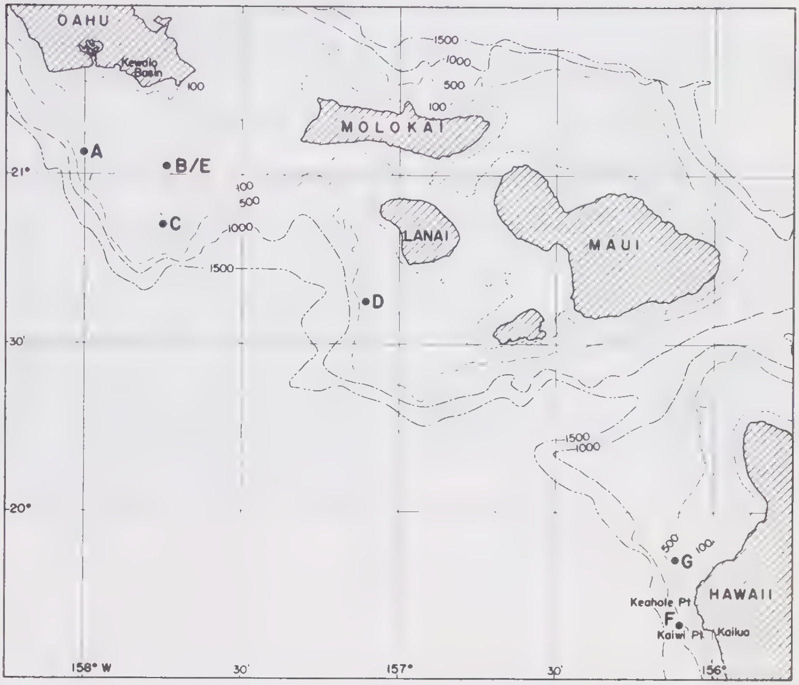

Figure 6.—Fish aggregating devices off Oahu, Lanai, and Hawaii.

The buoy design was adequate at all sites, except D, where unforeseen strong currents occurred twice during the testing period. On both occasions the current forced the buoy to submerge and caused the anchor to be dragged along the relatively flat, mud and silt bottom.

The buoys off Kona (F and G) were not part of the original buoy project. Consequently, wooden rafts that were available from a prior experiment were used instead of the steel-drum buoys. These rafts remained operative for 10 months before breaking apart during the same series of storms that caused the losses of A and D buoys. The winds off Kona exceeded 40 knots during this storm.

The drapes of fine-mesh netting used on F and G buoys were very effective in attracting fish; however, they also gilled numerous mackerel scad, *Decapterus punctatus* (Fig. 7), and were torn to shreds from sharks feeding on the gilled fish.

Monitoring Trips

Visits to the buoys were interrupted at various times, either because of rough sea conditions or loss of buoys (Table 1). Sixteen visits were made to A, 13 to B, 13 to C, and 10 to D. The catch by trolling on these trips was generally low at all the buoys. The total catch consisted of 29 fish at A (1.8 fish per visit), 11 at B (0.8 fish per visit), 3 at C (0.2 fish per visit), and 7 at D (0.7 fish per visit). The low catch was largely due to fishing by trollers prior to the arrival of the monitoring vessel. Consequently, determination of the presence of fish around the buoys were made from fish and bird flock sightings and fish-finder observations. Fish were present at A and 13 of 16 visits (81.2 percent), at B on 8 of 13 visits (61.5 percent), at C on 6 of 13 visits (46.2 percent), and at D on 9 of 10 visits (90.0 percent). Thus, buoys A and D, because of their locations (see Discussion), were more effective in attracting fish than B and C.

To determine the effectiveness of the buoys statistically, controlled fishing by trolling was done within 0.5 mile and at distances of 3 to 5 miles from the buoys

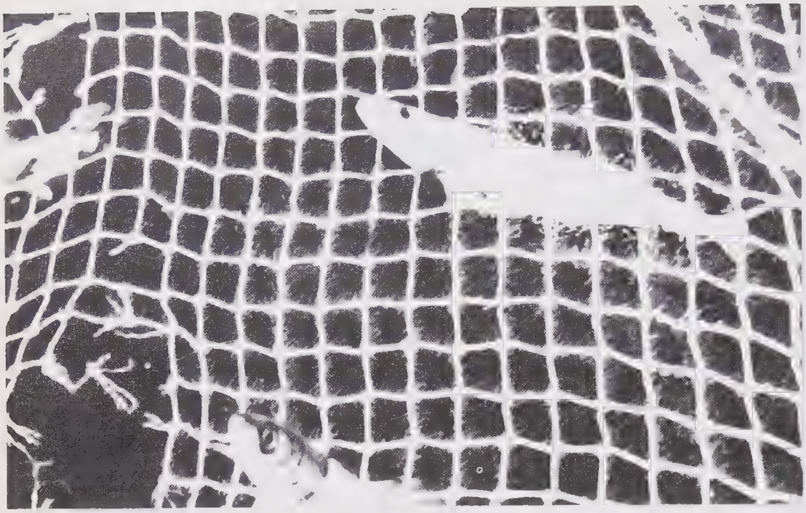

Figure 7.—Mackerel scad gilled on netting hung from fish aggregating device. Torn sections caused by shark attacks on gilled fish.

by a commercial trolling boat and vessels used in monitoring the buoys. Because of differences in fishing duration and in number of lines fished by different vessels, catch-per-line-hour was used in comparing the effect of the buoys in the two areas. Sixteen pairs of observations were obtained in March, April, and August 1978. Of these, fish were caught within 0.5 mile of the buoy on nine occasions, between 3 and 5 miles on one occasion, and in both areas on one occasion. No fish was caught in both areas on five occasions. There were 10 positive differences in the catch rates in favor of the buoy area, 1 negative difference, and 5 with no difference.

The randomized test for matched pairs (Siegel, 1956) indicated that catch rates within 0.5 mile of the buoys were significantly greater ($P = 0.00097$, one-tailed) than in areas 3 to 5 miles away. The test, thus, indicated that the buoys were successful in aggregating fish.

Pole-and-Line Fishing

The buoys were first deployed in May, at the beginning of the skipjack tuna fishing season. The anticipated visits to the buoys by pole-and-line boats during the fishing season did not occur because of the unexpected loss of all four buoys in July and because the buoys could not be reinstalled before the end of the fishing season. All four buoys were reinstalled between August and October, and visits by pole-and-line boats began in December. Initially, the few boats that fished around the buoys were reluctant to report their visits and catches because they did not want other boats to visit the buoys also. The reporting of visits and catches improved with time, however, as the effectiveness of the buoys became common knowledge throughout the fishing fleet.

Several of the smaller bait boats visited the buoys more often than the others. These boats usually left port well before daybreak in order to be at the buoy site by sunrise. They began fishing at the buoys at daybreak and pursued the schools as the latter departed from the immediate area of the buoys. As fishing slacked off, the boats departed the area to seek schools of larger fish. Depending on the day's catch, these boats visited the buoys again in late afternoon before returning to port. Occasionally when fishing around the buoys was exceptionally good, these boats returned to port well before noon with catches of 10,000 pounds, or more.

During 1978, the number of known visits increased from a low of 9 in January to 80 in May (Table 2), representing 5.6 and 46.8 percent, respectively, of the total monthly fishing trips made by the fleet of 12 pole-and-line boats. The ratio of visits to total trips peaked in April, decreased sharply in June, and remained low throughout the remainder of the year. This was reflected in the total monthly catches around the buoys. The sharp increase in catch at the buoys in April corresponded with the start of the fishing season when season fish (medium and large skipjack tuna) entered the fishery. The significant drop in the monthly catches around the buoys in June, July, and August was due to reduced visits to the buoys as a result of the presence of these season fish in areas away from the buoys. Because these fish commanded two and three times more per unit price of small fish which predominated in the catch around the buoys, they drew the boats away from the buoy sites.

The high catches of 424,897 pounds in April and 431,129 pounds in May represented 58.4 and 43.3 percent of the respective total cannery landings. During this period, there were 23 catches of over 10,000 pounds, 2 catches of over 20,000 pounds, and 2 catches of over 30,000 pounds. (One boat reported catches of nearly 60,000 pounds in a 3-day period.) The average catch per visit was 7,326 pounds in April and 5,389 pounds in May.

Fish species taken by pole-and-line boats at the buoys (Table 3) included skipjack tuna (89.7 percent), yellowfin tuna (9.3 percent), kawakawa (0.6 percent), and dolphin (0.3 percent). The skipjack tuna ranged in size from 2 to 12 pounds, with occasional catches of large fish above 20 pounds. Small yellowfin tuna and kawakawa ranged in size from 2 to 12 pounds and dolphin from 10 to 30 pounds. Skipjack tuna were taken at all four sites, but mostly at A and D. The single recorded visit to B consisted of a catch from one skipjack tuna school. Yellowfin tuna were taken mostly at D, with a fair amount at A, and a small amount at C. Kawakawa were taken at these three sites also, but the bulk of the catches were made at C.

The pattern of visits and catches in 1979 did not follow that of the previous

Table 1.—Visits and observations at monitored buoys.

	A							B						
Date	Time	Line hours trolled	Catch	Catch per line hour	Fish seen[1]	Bird flock (No. birds)	Fish finder[2]	Time	Line hours trolled	Catch	Catch per line hour	Fish seen[1]	Bird flock (No. birds)	Fish finder[2]
1977														
May 26	1600	0.50	0	0.00	1	0	—	0845	0.33	1	3.03	0	20	—
June 14-15	0828	1.42	0	0.00	3	0	F-15	1103	1.42	1	0.72	3	0	0
July 2-3				Buoy lost 1 July				1130	1.50	1	0.67	0	0	F-20
July 17								1025	2.25	0	0.00	1	0	0
Aug.				Replaced 8 Aug.							Buoy lost 20 July			
Sept. 12	1015	0.67	0	0.00	1	250	S-15, 25				Replaced 27 Sept.			
Oct. 19	1026	0.60	0	0.00	0	0	F-16	1256	0.27	0	0.00	0	0	—
Nov. 19-20	1235	1.50	0	0.00	1	15	0	1535	0.95	0	0.00	0	0	0
Dec. 15-16	1325	1.15	0	0.00	0	0	0				Buoy lost 2 Dec			
1978														
Jan. 23	0926	1.00	0	0.00	0	0	0							
Feb.				No visit[3]							Buoy lost 2 Dec			
Mar. 21-23	0738	1.15	1	0.87	0	0	—				Replaced 20 March			
Apr. 13-14	0700	4.00	6	1.50	TS	1,000	—	0835	1.67	0	0.00	0	15	0
May 30-31				No visit				0925	0.67	0	0.00	2	0	—
June 1	0735	1.33	0	0.00	1	150	—				No visit			
July				No visit[3]							No visit[3]			
Aug. 17-18	1030	2.50	0	0.00	0	0	—	1010	4.58	7	1.53	0	25	—
Sept 20-21	0825	0.75	0	0.00	TS	10	—	0950	0.75	0	0.00	1	0	—
Oct.				No visit[3]							No visit[3]			
Nov				No visit[3]							No visit[3]			
Dec.				Buoy lost 26 Dec.							No visit[3]			
1979														
Jan.				Buoy lost							No visit[3]			
Feb.				Buoy lost							No visit[3]			
Mar. 6				Replaced 31 Mar.				1005	0.67	0	0.00	0	0	—
Apr. 11				No visit				0752	0.50	0	0.00	0	0	—
May				No visit							No visit			
June 1	0750	2.33	2	0.86	TS	300	S-15				No visit			
June 29	0700	3.50	6	1.71	TS	200	0				No visit			
July 10	0615	2.67	13	4.87	0	0	0				No visit			
July 10				No visit				0805	5.33	1	0.19	0	0	0
July 31	1700	8.00	1	0.13	0	20	—				No visit			
Aug				Buoy lost 8 Aug (terminated)							Buoy lost 8 Aug (terminated)			

	C							D						
Date	Time	Line hours trolled	Catch	Catch per line hour	Fish seen[1]	Bird flock (No birds)	Fish finder[2]	Time	Line hours trolled	Catch	Catch per line hour	Fish seen[1]	Bird flock (No birds)	Fish finder[2]
1977														
May 26	1100	0.50	0	0.00	4	50	—				No visit			
June 14-15	1304	1.33	0	0.00	1	60	—	0630	1.25	0	0.00	3	0	0
July 2-3	0700	1.40	0	0.00	2	40	0	0815	4.50	6	1.33	18	45	0
July 17	1200	1.25	0	0.00	7	0	0				No visit			
Aug				Buoy lost 20 July							Buoy lost 20 July			
Sept 12														
Oct. 19				Replaced 19 Oct.							Replaced 19 Oct			
Nov. 19-20	0700	0.85	0	0.00	0	0	0	1330	1.10	0	0.00	6	0	S-10
Dec 15-16	1450	1.00	0	0.00	0	0	0	0640	1.70	0	0.00	TS	100	—
1978														
Jan 23	1230	0.93	0	0.00	0	0	0	1750	0.67	0	0.00	0	0	0
Feb.				No visit[3]							No visit[3]			
Mar 21-23	0612	1.40	1	0.71	0	0	—	1537	0.65	0	0.00	10	75	—
Apr. 13-14	1810	1.25	0	0.00	0	0	0	1341	2.00	0	0.00	TS	25	—
May 30-31	1043	0.80	0	0.00	0	0	—	1445	2.33	0	0.00	TS	50	—
June 1				No visit							No visit			
July				No visit[3]							No visit[3]			
Aug 17-18	0735	2.50	1	0.40	0	0	—	1715	6.25	1	0.16	0	100	—
Sept 20-21	1210	1.25	0	0.00	0	0	—	1652	1.50	0	0.00	TS	30	—
Oct.				No visit[3]							No visit[3]			
Nov				No visit[3]							No visit[3]			
Dec.				No visit[3]							No visit[3]			
1979														
Jan				No visit[3]							No visit[3]			
Feb				No visit[3]							Buoy lost 26 Feb (terminated)			
Mar 6	1145	0.75	0	0.00	0	0	—	—	—	—	—	—	—	—
Apr 11	0938	0.33	1	3.03	0	0	—	—	—	—	—	—	—	—
May				No visit				—	—	—	—	—	—	—
June 1				Buoy lost 10 June (terminated)										
June 29	—	—	—	—	—	—	—	—	—	—	—	—	—	—

[1] TS=tuna school
[2] Scattered fish (F) or school (S) at stated depth in fathoms
[3] No visits to buoys due to rough seas

Table 2.—Monthly catches (in pounds) of tuna by pole-and-line boats during fish aggregating device experiment.

	Buoy															
Year/ month	A		B		C		D		Totals		Catch per visit	Landings by fleet	Trips by fleet	Catch per trip	Percent buoy visit	Percent buoy catch
	Catch	Visit	Catch	Visit	Catch	Visit	Catch	Visit	Catch	Visit						
1977																
Dec.	10,000	1	—	—	—	—	25,200	2	35,200	3	11,733.3	226,622	126	1,798.6	2.4	15.5
1978																
Jan.	9,000	2	—	—	18,600	3	13,938	4	41,538	9	4,615.3	410,210	160	2,563.8	5.6	10.1
Feb.	7,849	7	—	—	1,396	2	40,085	20	49,330	29	1,701.0	143,522	111	1,292.9	26.1	34.4
Mar.	9,718	6	—	—	—	—	22,872	14	32,590	20	1,629.5	142,646	69	2,067.3	29.0	22.8
Apr.	86,738	14	5,110	1	88,734	9	224,315	34	424,897	58	7,325.8	727,933	109	6,678.3	53.2	58.4
May	208,288	48	—	—	—	—	222,841	32	431,129	80	5,389.1	996,312	171	5,826.4	46.8	43.2
June	31,503	7	—	—	—	—	—	—	31,503	7	4,500.4	909,456	183	4,969.7	3.8	3.5
July	28,109	9	—	—	—	—	—	—	28,109	9	3,123.2	869,491	166	5,237.9	5.4	3.2
Aug.	—	—	—	—	—	—	23,170	5	23,170	5	4,634.0	571,981	125	4,575.8	4.0	4.1
Sept.	—	—	—	—	—	—	30,725	9	30,725	9	3,413.9	251,363	80	3,142.0	11.2	12.2
Oct.	—	—	—	—	—	—	22,882	9	22,882	9	2,542.4	341,885	97	3,524.6	9.3	6 7
Nov.	—	—	—	—	—	—	34,162	12	34,162	12	2,846.8	471,969	107	4,410.9	11.2	7.2
Dec.	—	—	—	—	—	—	—	—	—	—	—	218,450	76	2,874.3	—	—
Total	381,205	93	5,110	1	108,730	14	654,990	139	1,150,035	247	4,656.0	6,055,218	1,454	4,164.5	17.0	19.0
1979																
Jan.	Buoy lost		—	—	—	—	—	—	—	—	—	113,050	47	2,405.3	—	—
Feb.			—	—	—	—	—	—	—	—	—	220,540	74	2,980.3	—	—
Mar.			—	—	—	—	Buoy lost		—	—	—	258,607	74	3,494.7	—	—
Apr.	Buoy replaced		—	—	—	—			—	—	—	280,668	109	2,574.9	—	—
May	10,500	5	—	—	—	—			10,500	5	2,100.0	1,045,667	176	5,941.3	2.8	1.0
June	18,841	5	—	—	Buoy lost				18,841	5	3,768.2	827,293	187	4,424.0	2 7	2.3
July	4,200	3	—	—					4,200	3	1,400.0	1,012,239	184	5,501.3	1.6	0.4
Aug.	Buoy lost		Buoy lost						—	—	—	—	—	—	—	—
Total	33,541	13	—	—	—	—	—	—	33,541	13	2,580.1	3,758,064	851	4,416.1	1.5	0 9

Table 3.—Fish species caught (in pounds) by pole-and-line boats around fish aggregating buoys during 1978.

		Species									
		Skipjack tuna		Yellowfin tuna		Kawakawa		Dolphin		Total	
Buoy	Visits	Catch	Catch per visit	Catch	Catch per visit	Catch	Catch per visit	Catch	Catch per visit	Catch	Catch per visit
A	92	357,044	3,880 4	22,682	246.5	1,479	16.0	854	9.3	382,031	4,152.5
B	1	5,110	5,110.0	0	0.0	0	0.0	0	0.0	5,110	5,110.0
C	14	103,037	7,359.8	1,475	105.4	4,218	301.3	0	0.0	108,730	7,766 4
D	139	573,106	4,123 1	80,183	576.9	1,706	12.3	3,034	22.6	658,029	4,734 0
Total	246	1,038,297	4,220.7	104,340	424 1	7,403	30.0	3,888	15.8	1,153,900	4,690.6
Percent of total catch		89 73		9.28		0 64		0.34		99.99	

year for several reasons. First, the presence of large skipjack tuna in the fishery in late fall and winter kept the boats from returning to the buoys in the off-season; second, the December-January period was beset with inclement weather, including several periods of gale-force winds that reduced fishing activity considerably; and third, the loss of buoys A in December 1978 and D in March resulted in the elimination of the two buoys that were most productive of tunas. By the time A was restored in April and the 2-5 weeks necessary for it to become effective had gone by, the regular skipjack tuna fishing season was at hand, and the pole-and-line boats had already turned their attention to large fish away from the buoy areas.

Troll Fishing

Table 4 lists the visits and catches obtained from interviews with trolling boat operators. Only visits to A, B, and C are shown because D, located off Lanai, was beyond the usual 1-day charter range of most trollers based at Kewalo Basin, and because no firm reports were received from boats fishing at this buoy out of Maui and Lanai. Since most of the boats at Kewalo Basin fished irregular schedules and since it was not always possible to interview all boats daily, the number of visits and resultant catches may be greatly understated.

Visits to the buoys generally remained low (8.3 visits per month) during the last half of 1977 due to interruption of fishing caused by buoy losses, rough sea conditions, and poor initial response in reporting by the trollers. Buoy visits increased to 22 visits per month in 1978 and to 44 visits per month in 1979.

During the 26-month period of fishing around the buoys, a total of 2,087 fish, estimated at 29,351 pounds, were taken by trolling boats. The catch rate for the period was 3.44 fish per visit. Although the amount of fish taken was not overwhelming, the buoys, nevertheless, substantially reduced the number of zero-catch days (interviews with boat operators). From April through July 1978, the period of greatest fish concentration around the buoys, trollers caught 876 fish (estimated weight 11,288 pounds) at a catch rate of 10.55 fish per visit. The concentrations of fish around the buoys were not as great during the same period in 1979. Only 546 fish (estimated weight 10,156 pounds) were caught at a catch rate of 2.92 fish per visit. Both catch and catch rate were affected greatly by reduced fishing at A, the most productive buoy, which was lost in December 1978 and was not replaced until March 1979.

Fishing effort varied at the different buoy sites. Buoy A was visited most often (51.0 percent of all buoy visits) and yielded the most catch (61.5 percent of total buoy catch). Buoy B received 26.4 percent of all visits and yielded 17.7 percent of the total buoy catch, and buoy C recorded 22.6 percent of all visits and yielded 20.8 percent of the catch. Although buoys B and C were not productive of tunas, they were ideally placed to attract dolphin from nearby Penguin Bank. Several boats that preferred trolling for dolphin made regular visits to these sites. The catch rate of dolphin at these two sites averaged 1.87 fish per visit, as compared with 0.70 fish per visit to A.

Twelve species of fish were taken by trollers around the buoys (Table 5). Dolphin comprised the largest group (37.0 percent), followed by yellowfin tuna (25.9 percent), and skipjack tuna (23.0 percent). Of the 772 dolphin taken, nearly 72 percent were from sites B and C in roughly equal amounts; and of the 481 skipjack tuna and 540 yellowfin tuna taken, nearly 88 and 90 percent, respectively, were from site A.

Kawakawa represented 9.0 percent of the total catch, with roughly 41 percent taken from A, 36 percent from B, and 23 percent from C. Marlins, *Makaira nigricans* and *Tetrapturus audax*, and

Table 4.—Fish caught by trolling boats based at Kewalo Basin.

Year/ month	A Visit	A No of fish	A Wt. (lb)	B Visit	B No. of fish	B Wt. (lb)	C Visit	C No. of fish	C Wt (lb)	All buoys Visit	All buoys No. of fish	All buoys Wt (lb)	Catch per visit
1977													
June	8	18	475	3	0	0	4	1	5	15	19	480	1.26
July	—	—	—	5	57	335	1	11	55	6	68	390	11.33
Aug.	2	0	0	—	—	—	—	—	—	2	0	0	0.00
Sept.	2	4	25	—	—	—	—	—	—	2	4	25	2.00
Oct	12	89	187	7	22	170	1	0	0	20	110	357	5.55
Nov	2	1	10	2	3	40	1	0	0	5	4	50	0.80
Dec.	—	—	—	—	—	—	—	—	—	—	—	—	—
Total	26	112	697	17	82	545	7	12	60	50	206	1,302	4.12
1978													
Jan	9	52	327	—	—	—	7	61	439	16	113	766	7.06
Feb	9	29	216	—	—	—	7	3	26	16	32	242	2.00
March	6	6	272	—	—	—	5	3	50	11	9	322	0.82
April	14	236	2,499	3	5	84	6	38	395	23	279	2,978	12.13
May	19	294	4,083	8	23	363	9	129	992	36	446	5,438	12.39
June	6	35	431	4	32	452	4	33	591	14	100	1,474	7.14
July	7	45	1,340	1	2	16	2	4	42	10	51	1,398	5.10
Aug	11	14	327	1	7	42	5	17	148	17	38	517	2.24
Sept.	5	17	1,001	1	2	38	—	—	—	6	19	1,039	3.17
Oct.	31	26	953	8	9	152	12	6	105	51	41	1,210	0.80
Nov	37	33	210	8	10	135	6	6	165	51	49	510	0.96
Dec	3	10	250	8	1	6	6	2	15	17	13	271	0.76
Total	157	797	11,933	42	91	1,288	69	302	2,944	268	1,190	16,165	4.44
1979													
Jan.	—	—	—	11	18	189	10	21	205	21	39	394	1.85
Feb	—	—	—	37	69	1,705	15	18	322	52	87	2,027	1.67
March	10	4	51	16	15	180	12	4	48	28	19	228	0.68
April	10	4	51	7	11	144	8	14	171	25	29	366	1.16
May	59	189	2,582	15	36	594	15	61	2,076	89	286	5,252	3.21
June	27	136	1,551	6	22	434	1	3	60	34	161	2,045	4.74
July	30	45	1,315	9	25	257	—	—	—	39	70	1,572	1.79
Total	126	374	5,499	101	196	3,503	61	121	2,882	288	691	11,884	2.40
Total for period	309	1,283	18,129	160	369	5,336	137	435	5,886	606	2,087	29,351	3.44
Percent of all FAD totals	51.0	61.5	61.8	26.4	17.7	18.2	22.6	20.8	20.0				

Table 5.—Species and number of fish caught by trolling boats around fish aggregating buoys, May 1977-July 1979.

Species	Buoy A Visit	Buoy A Catch	Buoy A Catch/ visit	Buoy B Visit	Buoy B Catch	Buoy B Catch/ visit	Buoy C Visit	Buoy C Catch	Buoy C Catch/ visit	Total Visit	Total Catch	Total Catch/ visit	Percent of total
Skipjack tuna	309	423	1.37	160	3	0.02	137	55	0.40	606	481	0.79	23.0
Yellowfin tuna		484	1.57		12	0.08		44	0.32		540	0.89	25.9
Bigeye tuna		11	0.04		0	0.00		10	0.07		21	0.04	1.0
Kawakawa		77	0.25		68	0.42		43	0.31		188	0.31	9.0
Dolphin		217	0.70		275	1.72		280	2.04		772	1.27	37.0
Wahoo		30	0.10		8	0.05		2	0.02		40	0.07	1.9
Blue marlin		15	0.05		3	0.02		1	0.01		19	0.03	0.9
Striped marlin		2	0.01		0	0.00		0	0.00		2	0.01	0.1
Spearfish		3	0.01		0	0.00		0	0.00		3	0.01	0.1
Rainbow runner		16	0.05		0	0.00		0	0.00		16	0.03	0.8
Greater amberjack		3	0.01		0	0.00		0	0.00		3	0.01	0.1
Barracuda		2	0.01		0	0.00		0	0.00		2	0.01	0.1
Total	309	1,283	4.15	160	369	2.31	137	435	3.18	606	2,087	3.44	

shortbill spearfish, *T. angustirostris*, represented 1.2 percent of the total catch. Nearly all (83.3 percent) were taken at site A. All other fish, including bigeye tuna, *Thunnus obesus*; wahoo; rainbow runner, *Elagatis bipinnulata*; amberjack, *Seriola dumerili*; and barracuda, *Sphyraena argentea*, comprised 3.9 percent of the total catch. All bigeye tuna, except 10, were taken at A. The billfishes were generally taken about 0.5 to 1.5 miles away from the buoy, whereas the skipjack and yellowfin tunas were caught all the way from the buoy up to 3-5 miles away. Most of the other species were taken within 200-300 yards of the buoy.

Table 6. — Underwater observations of fish at fish aggregating buoys off Lanai and Kona, Hawaii.

Date	Buoy	Locality	Fish observed	Estimated number	Est. fish size (lb)	Depth range (m)
1977 15 Dec.	D	Lanai	Dolphin	14-16	15-20	0-35
			Sea chub, *Kyphosus cinerascens*	50-100		N.s.[1]
			Scrawled filefish, *Aluterus scriptus*	2	1	N.s.
1978 30 May	D	Lanai	Yellowfin tuna	800-1,000	6-8	0->50
			Dolphin	10-12	10-15	0->35
			Rainbow runner	15-20	<1	0->35
			Rough triggerfish, *Canthidermis maculatus*	80		N.s.
			Porpoises	12		
27 July	F	Kona	Skipjack tuna	200-300	2-10	0->70
			Yellowfin tuna	6		>50
			Bigeye tuna	1		
			Wahoo	3	15-20	15
			Rainbow runner	6		0-35
			Mackerel scad	>5,000		0->70
			Freckled driftfish, *Psenes cyanophrys*	50		N.s.
			Rough triggerfish	4		N.s
			Pilotfish, *Naucrates ductor*	2		N.s.
12 Aug.	F	Kona	Skipjack tuna	Many 1,000's	2-10	0->70
			Bigeye tuna	3	20-30	>35
			Rainbow runner	12		0-70
			Mackerel scad	Many 1,000's		0-70
			Freckled driftfish	200-300		N.s
			Rough triggerfish	12		0-35
1979 10 Aug.	F	Kona	Wahoo	2	10-15	0-35
			Rainbow runner	4		0-35
			Mackerel scad	1,000		0-35
			Greater amberjack	5	Juvenile	N.s.
			Rough triggerfish	60		N.s

[1] N s. = near surface

Occasional reports from Maui indicated heavy fishing activity around buoy D, where individual boat catches of 300-700 pounds of skipjack (8-10 pound size) and yellowfin (30-50 pound size) tunas, and 100 pounds of dolphin per weekend were commonly made in April 1978.

Reports from Kona indicated the success of the buoys placed there. Buoy F, in particular, which had been placed at the edge of an outstanding fishing area, was teeming with skipjack and yellowfin tunas within 5 weeks after deployment. Trollers were able to catch small skipjack tuna for marlin bait in 10-15 minutes, compared with half a day or more before the buoy was in place. During the height of the summer marlin run, many trollers who took advantage of the accessibility of bait-size skipjack tuna at buoy F reported catches of three and four marlin a day. One boat reported catching 11 marlin in a period of 10 consecutive days of fishing, while another caught 20 marlin in 20 days.

Other Types of Fishing

The buoys off Kona also attracted many commercial skiff fishermen using the "drop-stone" method to fish for 50-200 pound yellowfin tuna usually accompanying porpoise schools. The gear is essentially a handline using 10- to 12-inch mackerel scad as bait. The hooked bait is laid on a smooth stone weighing about 2 pounds together with a package of mackerel scad chopped up and wrapped in a chum bag. Both bait and chum bag are bound to the stone by a few turns of the mainline and secured with a slipknot. The stone is lowered 30-60 fathoms and is jerked free to expose the bait and chum. Fishing was done by positioning the skiff in the path of a porpoise school and dropping the line as the school approached the skiff. The buoys enabled fishing during periods when porpoise schools were absent from the area.

One report in June 1978 indicated that up to 50 trolling and handline boats fishing at G brought in 35,000 pounds of yellowfin tuna and marlins on one weekend and that the drop-stone skiffs averaged from three to four yellowfin tuna per day.

Underwater Observation

Observations by divers were made on five occasions, twice at D and three times at F (Table 6). Dives were made generally to depths of 100 or 150 feet. Tuna schools were seen on one dive at D and two dives at F.

A yellowfin tuna school observed at D (Fig. 8), composed of 6-8 pound fish, roamed from beneath the buoy to distances of 0.5 mile or more repeatedly. Its roaming behavior may have been induced by the presence of porpoises. The school became more compact and moved about more rapidly each time a porpoise approached it.

The skipjack tuna schools observed at F behaved differently. On the first dive, 27 July 1978, groups of several hundred skipjack tuna rose to within 100 feet of the surface from below. The major skipjack tuna school was situated at depths beyond 250 feet beneath the buoy, beyond the visibility of the divers On the second dive, 12 August 1978, many thousands of skipjack tuna were constantly in view of the divers and on several occasions, part of the school was seen to pursue baitfish (mackerel scad) to the surface within 30 feet of the buoy.

Discussion

The study provided information concerning buoy design, tuna schools attracted to fish aggregating devices, and the influence these devices had in modi-

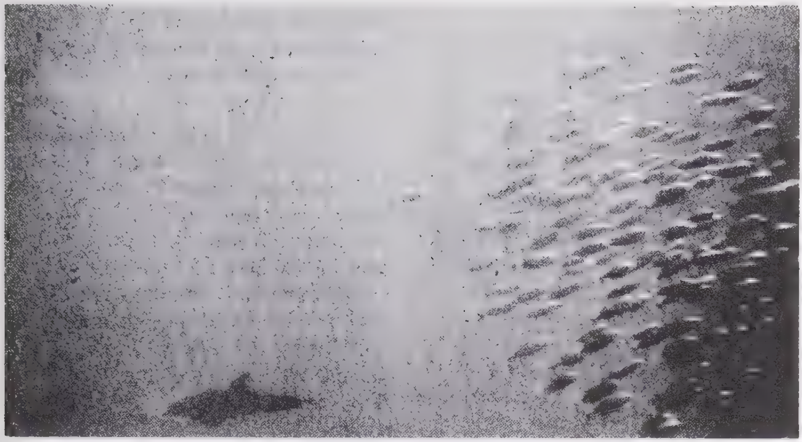

Figure 8.—Yellowfin tuna school accompanied by porpoise beneath fish aggregating device.

fying the established fishing routine in Hawaiian waters.

Buoy Design

For the most part, the buoys, as designed, performed adequately. However, the intermittent submerging and shifting of buoy D during periods of unusually strong tidal current indicated that the design was inadequate for that particular site. To prevent similar mishaps, the buoy should be enlarged to three steel drums and the anchor weight should be increased to 2,000-3,000 pounds. Other modifications include the relocation of the anchor line attachment to the apex of the forward V section and the addition of a 40-50 pound weight to the ballast pipe to prevent the buoy from leaning over.

The importance of the drape cannot be overemphasized. Although small fish of 2-5 inches tended to remain as close to the buoy as possible, and often strayed inside of the V section, it was mainly because of the drape that large fish remained at the buoy site over prolonged periods. The reduction of fish aggregations and catches at buoys that had lost the drapes were quickly noticed by the fishermen, who clamored for immediate restoration.

The drape should be made of material that can withstand the stresses of currents and heavy wave action. The drape made of ⅝-inch polypropylene rope was effective in attracting fish, as well as being long lasting; however, the drape need not encircle the buoy, as in our experiment. Five to seven lengths of rope hung vertically and seized onto horizontal bamboo crosspieces, spaced 3-5 feet apart, and short pieces of loosened rope strands attached at intervals of 24 inches to each length of rope, should make an adequate drape.

The buoy, as designed, was adequate for trolling and pole-and-line fishing. For purse seine fishing, however, the drape should be lengthened to about 100 feet, the chain at the top of the mooring line should be 120 feet long, and the position of the weight on the mooring line should be adjusted so that the upper loop of the buoyant rope will remain at a depth of 100 fathoms or more at all times.

Tuna Aggregations Around Buoys

Distribution by Size

The fish aggregating devices attracted all sizes of tunas ranging from below 2 to over 20 pounds. Small fish below 3-4 pounds (skipjack tuna, yellowfin funa, kawakawa, and a few bigeye tuna) generally remained in the immediate vicinity of the buoys and ranged in depth from the surface to over 250 feet. Larger fish, mainly skipjack and yellowfin tunas, roamed over wider areas from 0.25 to 3 miles or more from the buoys during the day. These fish apparently returned to the buoys at night since the day's first catches by bait boats were invariably made at the buoys at daybreak. The bait boats moved away from the buoys after sunrise as they continued to fish the schools.

Medium-sized yellowfin tuna, 30-50 pounds or more, and often exceeding 100 pounds, were caught on baited lines by either deep trolling at reduced speed or by handlining while drifting. These fish were caught anywhere within 1 mile of the buoys.

Other fish such as marlin and spearfish were usually taken by trollers at distances of up to 1.5 miles from the buoys, whereas dolphin were usually taken well within 100 feet of the buoys and up to 0.5 mile away.

Multiple Schools at Buoys

It was evident from the daily catch reports by bait boats that more than one tuna school was present around a buoy at the same time. During the height of fishing activity around the buoys (April and May 1978), from two to six bait boats reported catches from the same buoy on 30 separate days. It is likely that some of the catches were made at different times of the day, but because the best fishing usually occurred at sunrise, it was not uncommon for more than one boat to be at a buoy site well before daybreak and for all of them to commence fishing at sunrise. This was corroborated by trolling boat operators who repeatedly witnessed two or more bait boats fishing simultaneously, each on separate schools spaced up to 3 miles apart.

Length of Time at Buoys

In the absence of tagging effort, it was not possible to determine how long a tuna school or individual tuna remained at a buoy site. Catches made on consecutive days at the same buoy, however, indicate roughly the length of time fish school(s) remained around a buoy and were thus available to the fishermen.

Catches on consecutive days in 1978, the year visits to the buoys were most prevalent, are shown in Table 7. Nearly all of the 2 and 3 consecutive-day

Table 7. — Tunas caught on consecutive days at buoys A, C, and D during 1978.

	A			C			D		
Month	Consecutive days	Visits	Catch per day	Consecutive days	Visits	Catch per day	Consecutive days	Visits	Catch per day
Jan.	—	—	—	—	—	—	2	2	1,439
Feb	2	2	1,172	—	—	—	5	7	3,252
	3	3	1,256	—	—	—	6	11	3,564
March	3	4	2,080	—	—	—	2	2	1,267
April	—	—	—	—	—	—	2	2	2,775
	—	—	—	—	—	—	2	2	3,188
	—	—	—	—	—	—	3	3	2,417
	3	7	26,016	4	5	11,201	2	3	4,160
	2	3	1,192	—	—	—	9	21	23,341
May	5	9	9,690	—	—	—	9	26	23,141
	2	3	3,813	—	—	—	2	2	2,796
	13	32	10,602	—	—	—	—	—	—
	3	5	5,378	—	—	—	—	—	—
June	2	2	6,366	—	—	—	—	—	—
	2	3	5,689	—	—	—	—	—	—
July	2	2	3,256	—	—	—	—	—	—
	2	2	1,186	—	—	—	—	—	—
	2	2	2,919	—	—	—	—	—	—
Aug	—	—	—	—	—	—	—	—	—
Sept	—	—	—	—	—	—	4	4	2,730
Oct.	—	—	—	—	—	—	2	2	3,657
Nov.	—	—	—	—	—	—	4	4	3,570
	—	—	—	—	—	—	5	5	2,691
	—	—	—	—	—	—	2	2	2,901
December (no visits)									

catches listed represent visits to buoys made in anticipation of good catches. Visits usually ended after a couple of days whenever the catches were less than anticipated. Longer consecutive-day catch periods of 4-6 days indicate a continuation of visits due to good catches resulting from the presence of a large school or the accumulation of schools around the buoy. This occurred twice in February at buoy D, prior to the start of the fishing season, once in May at A, after the start of the fishing season, and once in September and twice in November at D, after the end of the season. During the early part of the season, when fish schools were abundant, the period of consecutive days fished extended to 13 days at buoy A and 18 days at D.

Thus, although the length of stay of individual tuna schools at a buoy site cannot be determined from these data, the arrival and accumulation of schools around the buoys enabled the fishing boats to fish continuously for periods of up to 2 and 3 weeks at a time.

Effect of Buoy Location

Pole-and-line catches at the different buoy sites varied considerably (Table 1). Buoys A and D, which were anchored in deep water within 2 miles of the 1,000-fathom ledge were particularly successful in attracting tuna schools. They commanded 93.9 percent of all reported visits in 1978 and yielded 90.1 percent of all tunas caught around the buoys.

Buoy C, anchored off the tip of Penguin Bank and located 6 miles away from the 1,000-fathom ledge, was only moderately successful. Most of the tuna catches there were made during a span of 1 week in both January and April.

Buoy B, anchored off Penguin Bank and 15 miles shoreward of the 1,000-fathom ledge, fared poorly, as it was fished only on one occasion. Since only visits resulting in catches were reported by bait boats, it is likely that more visits may have been made to B and C, as well as to A and D. Nevertheless, both B and C received little attention from these boats since they were located too close to Penguin Bank where schools of tunas were known to appear only occasionally.

Trolling boats based at Kewalo Basin which visited A, B, and C also recorded low catches of tunas at B and C (Table 5). Verbal reports of troll fishing at the two buoys placed off Kona indicated similar results. Buoy F, which was anchored at a depth of 1,250 fathoms, attracted large concentrations of skipjack and yellowfin tunas, but buoy G, which was anchored at a depth of 220 fathoms and 3.5 miles away from the 1,000-fathom ledge, was not as successful in attracting skipjack tuna schools.

The superior catches of skipjack tuna at buoys A, D, and F were apparently due to their placement at or near the 1,000-fathom depth contour. This was not surprising since we had known through interviews with both pole-and-line and troll fishermen prior to our selecting the buoy sites that large yellowfin tuna generally followed the 1,000-fathom contour in moving north and south along the leeward coasts of the islands. We suspected that schools of skipjack tuna would follow the same pattern.

Influence on Fishing Routine

Pole-and-Line Fishing

The usual fishing routine followed by bait boats was to spend 1 day, occasionally 2, fishing for baitfish and 1 or 2 days, sometimes 3, fishing for skipjack tuna. Consequently, 30-50 percent of the time was lost to baiting operations. Additional time was lost at sea due to scouting for tuna schools.

The introduction of the buoys eased the stringent demands on the supply and condition of baitfish and eliminated scouting time and time lost in pursuing schools. Night baiting often was sufficient to provide baitfish for a day's fishing. Consequently, fishing routine was reduced to baiting at night and fishing the next day. If the catch was sufficiently large, the boats would return to port well before noon and prepare for night baiting. Following this routine, many boats were able to fish 5 or 6 days a week. One boat fished 8 days during a 9-day period. On numerous occasions vessels visited buoy A with less than the minimum amount of baitfish normally required for a day's fishing, and with baitfish in slightly weakened condition because of the short distance from port, and fishing around it required less intensive chumming.

Troll Fishing

Trolling boats also modified their daily routine. They headed directly for the buoys in the morning and again on their way into port. Some trollers even changed their fishing method by either trolling deep with live bait at very low speed or drifting and fishing with light tackle or handlines.

Handline Fishing

In Kona, Hawaii, where handlining (drop-stone fishing) for medium to large yellowfin tuna has been going on for a number of years, the introduction of the buoys provided an additional dimension to fishing. In the past, daylight fishing for large yellowfin tuna accompanying porpoises was done by dropping lines in the midst of a school of porpoises. The porpoise schools usually passed through the area within a day or so. With the installation of the buoys, however, the porpoise schools remained in the area for many days at a time, circling the buoys at distances of 4-6 miles all day long.

A similar type of fishing called ikashibi fishing, is done off Hilo, Hawaii, where squid is used as bait, supplemented by mackerel scad (Yuen, 1979). Because live squid is used as the principal bait, fishing is done usually at night. The fishery, which began in 1973, shows promise of becoming an important segment of Hawaiian fisheries. The catch, consisting of bigeye and yellowfin tunas and, occasionally, albacore, increased from 89.0 t in 1973 to 154.6 t in 1975. This fishery could benefit from fish aggregating devices.

Buoy Benefits

It is not possible to determine precisely what the total pole-and-line catch might have been without the buoys in 1978, nor to what extent the buoys had increased the off-season catches because both monthly and year-to-year catches of the fishery fluctuate widely. There is no question, however, that the buoys were a boon to the pole-and-line fishermen, particularly with respect to more economical use of baitfish, to a reduction of time lost to baiting and searching for tuna schools, and to reduced fuel costs.

The buoy test, which was aimed primarily to aid the skipjack tuna fishery, resulted in two important side benefits. One was the heavy use of the buoys by trolling boats, the other was the utilization of the buoys by drop-stone commercial fishermen, who were able to extend the fishing of porpoise-associated tunas from one to several days and enabled fishing in the absence of porpoise schools.

Acknowledgements

We wish to thank the captain and crew of the MV *Easy Rider* and officers and crew of the NOAA ship *Townsend Cromwell* for their excellent cooperation in mooring the buoys and monitoring the fish catch data, and Shoji Teramoto, Honolulu Laboratory, for assistance in contacting tuna boat captains for information of fishing around the buoys. Special thanks go to George Parker, Kona charter boat owner, for the use of his boat to monitor and repair the buoys off Kona, Hawaii, and to Charles Spinney, Kona charter boat owner, for recovering and towing to safety a buoy that had been cut loose from its mooring.

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USING BOX-JENKINS MODELS TO FORECAST FISHERY DYNAMICS: IDENTIFICATION, ESTIMATION, AND CHECKING

ROY MENDELSSOHN[1]

ABSTRACT

Box-Jenkins models are suggested as appropriate models for forecasting fishery dynamics. Unlike standard production models, these models are empirical, dynamic, stochastic models. Box-Jenkins models are not biased when estimating relationships between catch and effort, as are standard production models. The use of these techniques is illustrated on catch and effort data for the skipjack tuna fleet in Hawaii. An actual 12-month forecast is shown to give a reasonable fit to the observed data. Most of the discrepancies are explained by changes in the behavior of the fishermen (i.e., economic factors), rather than by lack of knowledge of the behavior of fish.

Accurate forecasting models would be useful in fishery management because extended jurisdiction and international agreements require preseasonal predictions of the actual catch of a fleet. In addition, improved forecasts of fish availability can lead to improved planning by fishermen or by processing firms. Forecasting techniques have expanded greatly in the last years, but few have been adapted to research in fisheries management. Instead, techniques designed to establish the equilibrium health of the stocks are also being used to attempt dynamic forecasting.

At present, two least squares procedures are being used to estimate the general production model, the search procedure of Pella and Tomlinson (1969) and the weighted least squares of Fox (1970, 1971, 1975). The Fox procedure fits catch per unit effort against a function of lagged effort. Several authors (Chayes 1949; Eberhardt 1970; Atchley et al. 1976) have demonstrated that scaling the dependent variable (i.e., catch) by the independent variables (i.e., effort) biases the fit by introducing artificial correlation into the data. Johnston (1972) showed that ordinary least squares gave biased estimates and an inflated *F*-statistic when used with variables lagged on themselves. Neither the Fox nor the Pella-Tomlinson procedure accounts for the effect of autocorrelated errors in the estimation procedure which Granger and Newbold (1977) and Newbold and Davies (1978) have demonstrated bias both estimation and tests of fit. An examination of the residuals in Fox (1971, figure 3B) clearly shows them to be autocorrelated. Residuals from many spawner-recruit curves display similar behavior.

In this paper, the use of Box-Jenkins models for modeling and forecasting fisheries dynamics is explored. Box-Jenkins and other related forecasting techniques are specifically designed for estimating and testing models in the presence of autocorrelated errors. The fitted models are stochastic rather than deterministic, thus reflecting the variability found in most fisheries. The models are constructed empirically, and are best suited for forecasting. The models tell us little about the long-term health of the stocks, so that a judicious use of production, yield per recruit, and accurate forecasting models is required to give the best overall picture of the fishery.

My preference for Box-Jenkins models over other forecasting methods now available is due to the good documentation (see for example Anderson 1975; Box and Jenkins 1976; Granger and Newbold 1977) and computer accessibility. The results presented here were obtained using a package originally developed by David Pack at Ohio State University and now available through Automatic Forecasting Systems.[2]

The three-step process of model identification, model estimation, and model diagnostic checking is illustrated by developing a model that makes monthly forecasts of skipjack tuna, *Katsuwonus pelamis*, catches in Hawaii. Experience with the model suggests that for a 12-mo forecast of catch,

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[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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during peak months the forecast is within 15% of the observed catch (and is usually within 8-10% of the observed catch), most turning points in the catch trend are predicted, and the important feature of a low, flat catch during the summer months or high, peaked catches are accurately predicted. Moreover, the reasons for forecasts with large errors appear to be related more to fishermen's decisions in face of weather and economic factors, than to mispredicting the availability of the fish.

THE DATA AND UNDERLYING MODEL

The data to be analyzed are landings of skipjack tuna by approximately 12 boats from Oahu during 1964 through 1978. The raw data consist of the daily landings (each boat rarely stayed out more than a day or two), broken down by boat, and by four skipjack tuna size classes: large, medium, small, and extra small. For purposes of analysis, the data were aggregated into monthly totals, with the total number of fishing trips used as the measure of fishing effort. For monthly catch and effort during 1964-78 see Figures 1 and 2.

There are several causes for the observed seasonal variability. First, the tuna are only available in large numbers seasonally. Second, price considerations, particularly around Christmas and New Year when there is large demand, tend to spur fishing even when availability is low. Third, with only 12 boats fishing, if 1 or 2 boats are not able to fish for a few weeks, the catch will drop sharply. Finally, environmental factors, particularly weather (such as bad seas) will affect the landings since the boats are unable to fish.

Folklore in Hawaii has it that the catch remains similar each year, no matter how many boats fish. Comitini[3] examined the fishery using dummy variables and ordinary least squares to estimate

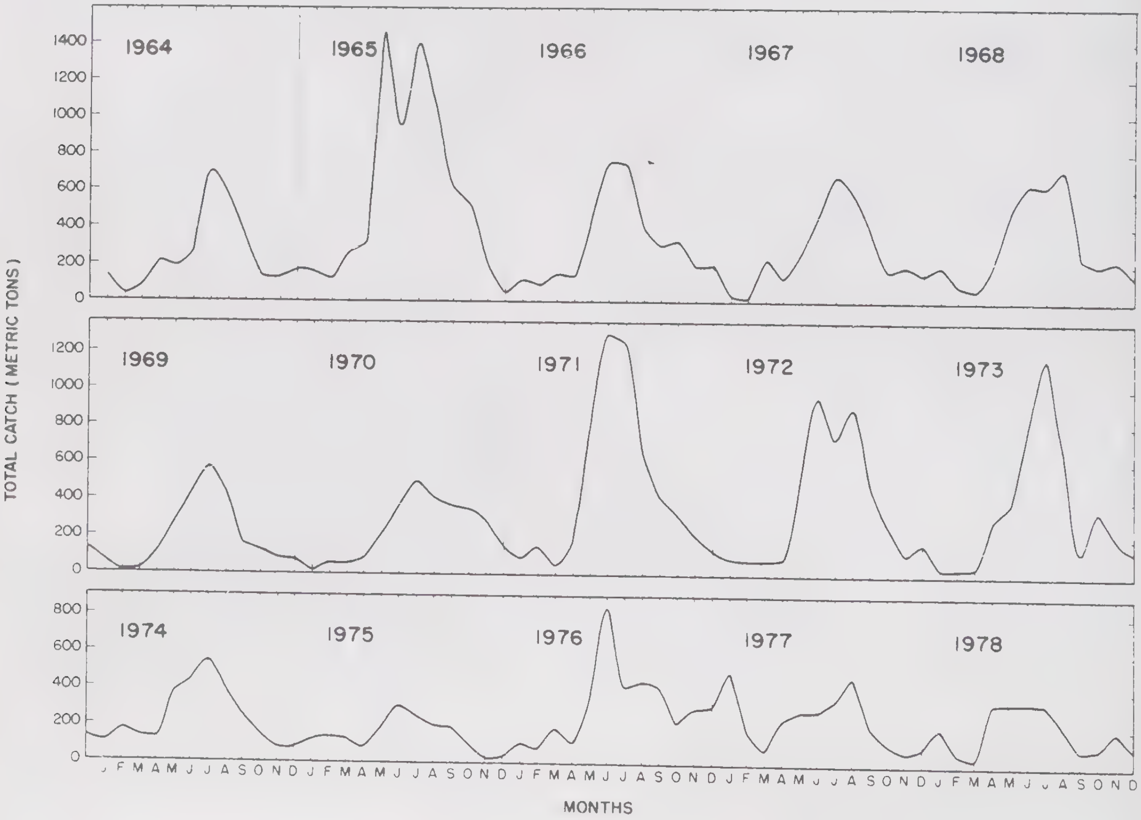

FIGURE 1.—Level of Hawaiian skipjack tuna catch by month, 1964-78.

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[3] Comitini, S. 1977. An economic analysis of the state of the Hawaiian skipjack tuna fishery. Sea Grant Tech. Rep. UNIHI-SEAGRANT-TR-78-01, 46 p.

a Cobbs-Douglas production function. He concluded, among other things, that natural fluctuations in resource availablity are significant, but did not include them in his analysis, nor did he provide a means for forecasting future catch. The National Marine Fisheries Service, using a regression model based on the previous year's catch, water temperature, and salinity at the start of the year, makes yearly predictions that have been mixed in accuracy.

Box-Jenkins models are autoregressive-integrated-moving-average models, or ARIMA models. These are linear, stochastic models that can describe fairly complex behavior, in contrast to Parrish and MacCall (1978) who use highly nonlinear equations to model the fluctuations in fishery data.

The modeling is based on the properties of stationary time series. A time series x_t is stationary if it has a constant mean, and if the covariance between events x_t, x_{t-s} depends only on s and not on t. Many series are stationary after removing a deterministic trend. Others are differenced in order to achieve stationary. Also, transforming the time series, particularly using the Box-Cox family of transformations, often improves the behavior of the time series. The initial step then is to transform and difference the data as necessary to achieve stationary. It is convenient to use the backshift operator B^j, where $B^j x_t = x_{t-j}$, to denote lagged variables. Given the new series $z_t = (1 - B^d)x_t$, a mixture of autoregressive and moving average models are sought. Autoregressive models are models that depend on the past history of the time series:

$$z_t = \phi_1 z_{t-1} + \phi_2 z_{t-2} + \ldots + \phi_p z_{t-p} + a_t$$

in terms of the backshift operator:

$$(1 - \phi_1 B - \phi_2 B^2 - \ldots - \phi_p B^p) z_t = a_t$$

while moving average models depend on past values of the noise or error:

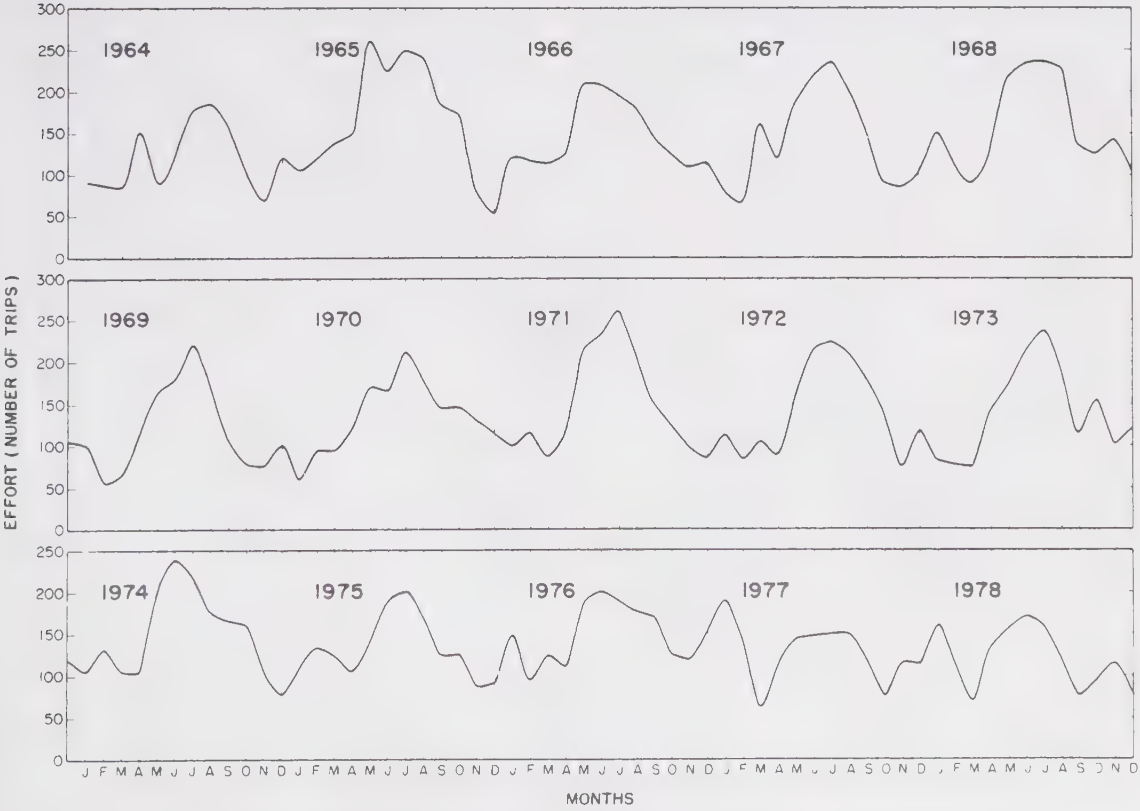

FIGURE 2.—Number of fishing trips per month by the Hawaii skipjack tuna fleet 1964-78, near Oahu, Hawaii.

$$z_t = a_t - \theta_1 a_{t-1} - \theta_2 a_{t-2} - \ldots - \theta_q a_{t-q}$$

or:

$$z_t = (1 - \theta_1 B - \theta_2 B^2 - \ldots - \theta_q B^q) a_t.$$

A model that has both moving average and autoregressive parameters is a mixed autoregressive moving average model, whose representation in terms of the backshift operator is:

$$(1 - \phi_1 B - \phi_2 B^2 - \ldots - \phi_p B^p)(1 - B)^d x_t$$

$$= (1 - \theta_1 B - \theta_2 B^2 - \ldots - \theta_q B^q) a_t.$$

MODEL IDENTIFICATION

The first step in the Box-Jenkins modeling process is to use properties of the data to tentatively identify a model. Even if a multivariate model (i.e., a model based on catch and effort) is the ultimate goal, univariate models of each series are constructed first. Often the univariate model produces forecasts that are almost as accurate as the multivariate model forecast.

My procedure was to identify, estimate, and check a series of models based on the data from January 1964 through July 1977. These models were used to forecast the already observed catch and effort for the period August 1977-December 1978. The models with the best "fit" were then reestimated to make the forecast for 1979. To make clear the feedback nature of identification, estimation, and checking in Box-Jenkins models, results from models fixed to 163 and 180 mo of data are intermingled, but clearly labeled.

A tentative model can be identified by estimating the autocorrelation and partial autocorrelation functions for each series. These are shown in Figures 3 and 4. Significant is the undamped sinusoidal behavior of each, with a period of 12 mo. Failure of both the autocorrelation and partial autocorrelation functions to go to zero is a sign of a nonstationary series, and the need for differencing. The 12-mo period suggested a yearly seasonal model, so that twelfth differences were taken, i.e., $z_t = (1 - B^{12}) x_t$.

The estimated autocorrelation and partial autocorrelation functions for the differenced catch and effort series are given in Tables 1 and 2. Following guidelines in appendix 9.1 in Box and Jenkins (1976), seasonal models with period s of the form:

$$z_t = (1 - \theta_1 B - \theta_2 B^2)(1 - \Theta_1 B^s) a_t \qquad (1a)$$

or $$z_t = (1 - \theta_1 B - \theta_2 B^2)$$

$$(1 - \Theta_1 B^s - \Theta_2 B^{2s}) a_t \qquad (1b)$$

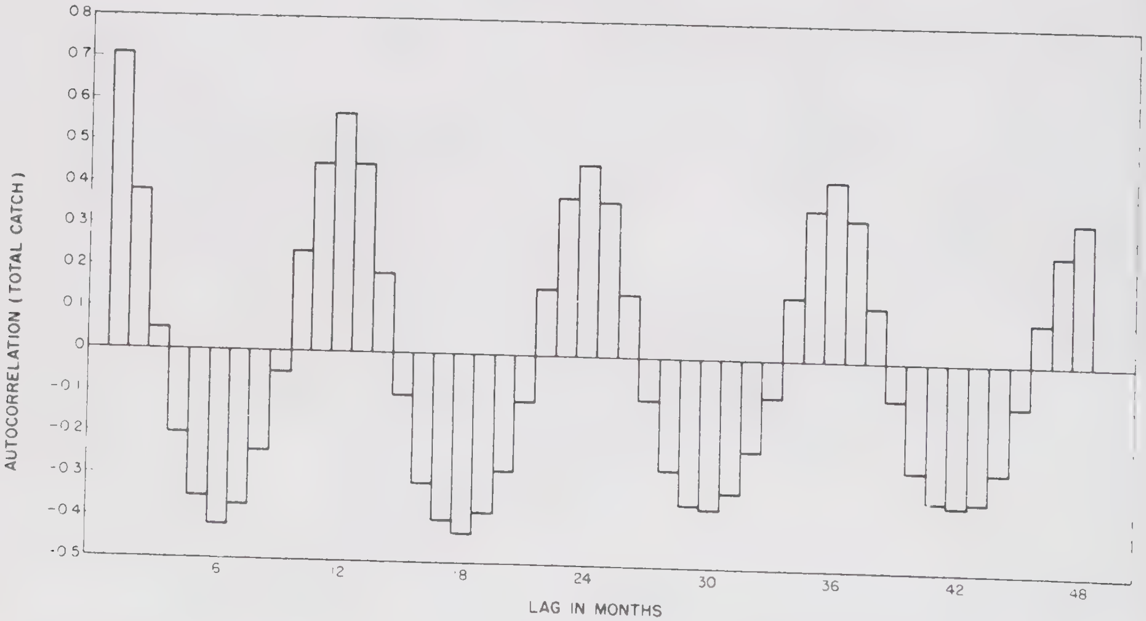

FIGURE 3.—Estimated total catch autocorrelation function for the catch of skipjack tuna near Oahu, Hawaii, 1964-78.

TABLE 1.—Autocorrelation functions for 12th differenced effort series of the Hawaii skipjack tuna fleet, 1964-78.

	Lag (mo)													
Item	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Regular auto.	0.39	0.17	0.20	0.16	0.10	0.04	0.03	0.07	-0.02	-0.08	-0.20	-0.45	-0.18	-0.08
SE	.08	.09	.10	.10	.10	.10	.10	.10	.10	.10	.10	.10	.12	.12
Partial auto.	.39	.03	.15	.03	.01	-.04	.00	.00	-.08	-.07	-.19	-.39	.15	.04
Item		15	16	17	18	19	20	21	22	23	24	25	26	27
Regular auto.		-0.18	-0.13	-0.12	-0.17	-0.15	-0.17	-0.12	0.05	0.04	0.02	0.00	-0.07	0.03
SE		.12	.12	12	.12	12	.12	.13	.13	.13	.13	.13	13	.13
Partial auto.		-.03	.02	-.07	-.14	-.01	-.02	-.05	.16	-.08	-.19	.05	-.12	03

TABLE 2.—Autocorrelation functions for 12th differenced catch series of the Hawaii skipjack tuna fleet, 1964-78.

	Lag (mo)													
Item	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Regular auto.	0.58	0.40	0.33	0.20	0.11	0.05	0.01	0.02	-0.06	-0.12	-0.21	-0.38	-0.21	-0 15
SE	.08	.11	.12	.12	.12	.12	.12	.12	.12	.12	.13	.13	14	14
Partial auto.	.58	.09	.10	-.07	-.03	-.04	- 00	.04	- 11	-.07	-.17	- 29	28	03
Item		15	16	17	18	19	20	21	22	23	24	25	26	27
Regular auto.		-0.16	-0.12	-0.08	-0.09	-0.08	-0.12	-0.10	-0.08	-0.08	-0.09	-0.06	-0 06	-0.05
SE		.14	.14	.14	.14	.14	14	.14	.14	14	14	.14	14	14
Partial auto.		-.01	-.06	-.02	-.07	.02	-.05	-.04	-.04	-.11	-.17	-.19	- 01	- 02

were hypothesized as the appropriate univariate models for both the catch and the effort time series.

ESTIMATION AND CHECKING

Given a tentative model, such as Model (1), the next step is a recursive procedure of estimating the parameters of the model, calculating the autocorrelation and partial autocorrelation functions of the residuals from the estimated model, and then testing the residuals for significant departure from the assumption that they are white noise. When a final model has been identi-

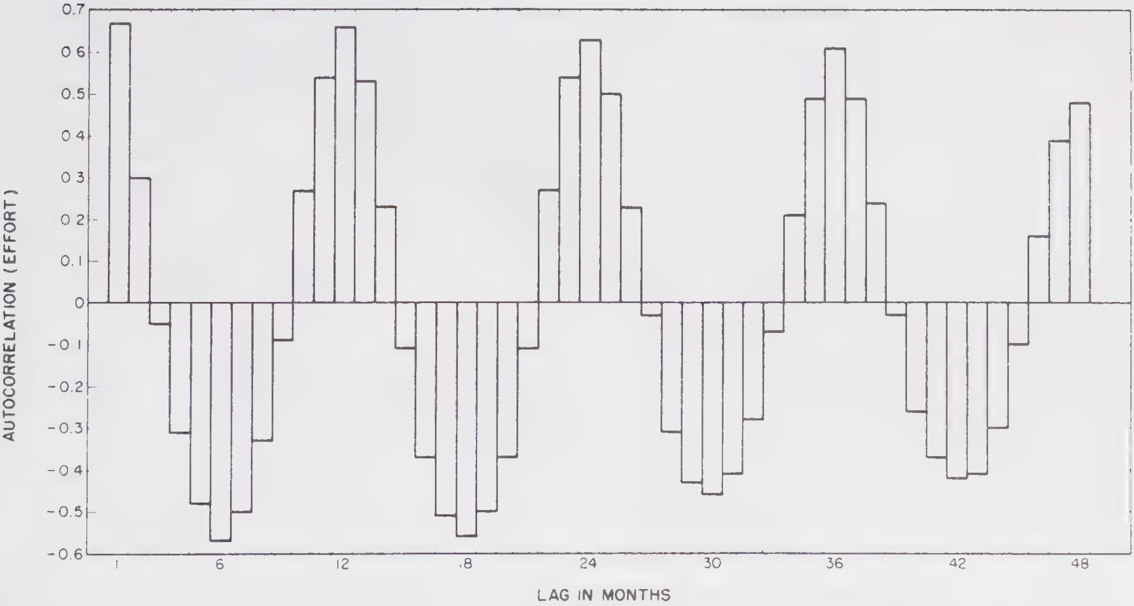

FIGURE 4.—Estimated effort autocorrelation function for the fishing trips by the Hawaii skipjack tuna fleet near Oahu, Hawaii, 1964-78.

fied, overfitting is tried, that is extra parameters are added to see if they are found to be not significantly different from zero.

To insure that I found the simplest model possible, I fitted first the model $z_t = (1 - \theta_1 B)(1 - \Theta_1 B^{12})a_t$, and then added parameters as seemed necessary based on the diagnostic checking. The estimates for Model (1) for catch and effort are given in Tables 3 and 4. Estimates using two estimation techniques, one using backforecasting and one suppressing it, are presented. Some programs do not have a backforecasting feature; my experience is that the estimated models obtained using backforecasting are far superior, as can be seen in the tables presented.

TABLE 3.—Parameter estimates for effort model, Model (1) (see text). (Based on 180 observations.)

Parameter	Estimate supressing backforecasting	SE	Estimate using backforecasting	SE
θ_1	−0.38349	0.07942	−0.44756	0.07886
θ_2	−.11326	.07996	−.12795	.07911
Θ_1	.5894	.08122	.99493	.00650
Θ_2	.00069	.08609	—	—
χ^2 statistic on residuals	26.894 with 44 df		37.319 with 45 df	
Residual mean square	1,018.60		755.270	
Residual SE	31.915		27.482	
Residual mean	1.629		0.5338	

TABLE 4.—Parameter estimates for catch model, Model (1) (see text). (Based on 163 observations.)

Parameter	Estimate suppressing backforecasting	SE
θ_1	−0.54100	0.08190
θ_2	−.22745	.08235
Θ_1	.75314	.08718
Θ_2	.05184	.09256
χ^2 statistic on residuals	27.470 with 43 df	
Residual mean square	165,410	
Residual SE	406.71	
Residual mean	17.506	

The estimated autocorrelation and partial autocorrelation functions of the residuals from both models are given in Tables 5 and 6. For the effort series, there is no sign of a lack of fit, while for the catch series terms of lag three or four are suggested. An overspecified model:

$$z_t = (1 - \theta_1 B^1 - \theta_2 B^2 - \theta_3 B^3 - \theta_4 B^4)(1 - \Theta_1 B^{12})a_t \quad (2)$$

was estimated for both the catch and effort time series. The results are summarized in Tables 7 and 8. The estimated autocorrelation and partial autocorrelation functions of the residuals (not shown) show no sign of additional lags or trend. The test statistic that the residual series are not significantly different from white noise gave no reason to doubt the models adequacy, and overfitting by including a $\Theta_2 B^{24}$ term found this term to be nonsignificant.

TRANSFER FUNCTION MODELS

If both the catch time series, say y_t, and the effort time series, say x_t, have been suitably transformed so that the resulting series are stationary, a transfer function of the form:

$$(1 - \delta_1 B - \delta_2 B^2 - \ldots - \delta_r B^r)x_t = (\omega_0 - \omega_1 B - \omega_2 B^2 - \ldots - \omega_s B^s)y_{t-b} + \eta_t$$

can be estimated where η_t is not assumed to be white noise, but itself can be modeled as an autoregressive-moving average process of a_t.

The procedures for identifying and estimating a transfer function model are similar to those for the univariate model, except that attention is focused on the estimated cross-correlation function between the "prewhitened" catch and effort series. Series are prewhitened if they are reduced to the residuals left from a given model. In this instance, both series are prewhitened by the univariate model for effort estimated in the preceding section. The estimated correlation function, impulse response function, and residual noise autocorrelation function are given in Table 9. The estimated autocorrelation function for the noise is similar to the original univariate autocorrelations, suggesting a noise model of the form:

$$\eta_t = (1 - \theta_1 B - \theta_2 B^2 - \theta_3 B^3 - \theta_4 B^4)(1 - \Theta_1 B^{12})a_t. \quad (3)$$

Based on guidelines in Box and Jenkins (1976:386-388) and knowledge of the fishery, two models were hypothesized:

$$(1 - B^{12})y_t = (\omega_0)(1 - B^{12})x_t + \eta_t \quad (4)$$

and: $$(1 - \delta_1 B - \delta_2 B^2)(1 - B^{12})y_t = (\omega_0 - \omega_1 B - \omega_2 B^2)(1 - B^{12})x_t + \eta_t. \quad (5)$$

Tables 10 and 11 summarize the estimates when

TABLE 5.—Estimated autocorrelation function for residuals of effort model for the Hawaii skipjack tuna fleet, 1964-78.

	Lag (mo)											
Item	1	2	3	4	5	6	7	8	9	10	11	12
Auto.	0.01	0.03	0.09	0.06	0.04	−0.11	−0.05	0.04	−0.09	0.02	0.03	−0.01
SE	.07	.07	.07	.08	.08	.08	.08	.08	.08	.08	.08	.08
	Lag (mo)											
Item	13	14	15	16	17	18	19	20	21	22	23	24
Auto.	0.05	−0.01	−0.04	−0.09	−0.08	−0.09	−0.07	−0.08	−0.16	0.10	0.07	−0.02
SE	.08	.08	.08	.08	.08	.08	.08	.08	.08	.08	.08	.08

TABLE 6.—Estimated autocorrelation function for residuals of catch model for the Hawaii skipjack tuna fleet, 1964-78.

	Lag (mo)											
Item	1	2	3	4	5	6	7	8	9	10	11	12
Auto.	0.04	0.11	0.23	0.06	0.06	−0.05	0.00	0.10	−0.03	0.04	0.01	0.00
SE	.08	.08	.08	.09	.09	.09	.09	.09	.09	.09	.09	.09
	Lag (mo)											
Item	13	14	15	16	17	18	19	20	21	22	23	24
Auto.	0.05	−0.01	−0.07	−0.01	−0.00	−0.04	0.00	−0.01	−0.06	0.01	−0.04	−0.03
SE	.09	.09	.09	.09	.09	.09	.09	.09	.09	.09	.09	.09

backforecasting is used in estimating the parameters for Models (4) and (5). The chi-square statistics show no reason to suspect model inadequacy. The residuals show no significant cross-correlation with total catch, when $1/\sqrt{180}$ (180 observations in the series) is used as a rough standard error. The residual autocorrelation function shows spikes around lag 15 that are higher than would be desired, but overall the fit is reasonable, and the model residuals could reasonably be modeled as white noise.

TABLE 7.—Parameter estimates for effort model, Model (2) (see text). (Based on 180 observations.)

Parameter	Estimate suppressing backforecasting	SE	Estimate using backforecasting	SE
θ_1	−0.36746	0.08004	−0.43862	0.07930
θ_2	−.14976	.08412	−.18144	.08590
θ_3	−.16111	.08458	−.15377	.08617
θ_4	−.17096	.08454	−.16298	.08593
θ_5	−.11547	.08089	−.17291	.07998
Θ_1	.59065	.06431	.99483	.00033
χ^2 statistic on residuals	20.696 with 42 df		27.494 with 42 df	
Residual mean square	1,000.40		752.67	
Residual SE	31.629		27.435	
Residual mean	82151		.35175	

TABLE 8.—Parameter estimates for catch model, Model (2) (see text). (Based on 180 observations.)

Parameter	Estimate suppressing backforecasting	SE	Estimate using backforecasting	SE
θ_1	−0.55368	0.07972	−0.53771	0.07462
θ_2	−.35882	.08989	−.43825	.07543
θ_3	−.33817	.09056	−.41197	.01144
θ_4	−.24282	.09012	−.30909	.07479
θ_5	−.12294	.07994	−.14974	.07440
Θ_1	.76951	.05062	99585	00825
χ^2 statistic on residuals	15.092 with 42 df		20.384 with 42 df	
Residual mean square	143,240		115,170	
Residual SE	378.47		339.37	
Residual mean	2.1150		3.3299	

DISCUSSION AND FORECASTS

Two transfer function models and one univariate model have been used to forecast the catch and effort in the skipjack tuna fishery during 1979. It is worth emphasizing that the original 12-mo forecasts were made in January 1979 and the updated forecasts were made in May 1979, so the reported results are true forecasts—there was no a priori knowledge of the data to help improve the "fit" of the forecasts. The original catch and effort forecasts are given in Tables 12 and 13 while the updated catch forecasts are given in Table 14.

The models used to produce the forecasts are best understood when written out in difference equation form. The univariate model for catch is:

$$y_t = y_{t-12} + (a_t + 0.538a_{t-1} + 0.438a_{t-2} + 0.412a_{t-3} + 0.309a_{t-4}) \qquad (6)$$

$$- (0.996a_{t-12} + 0.535a_{t-13} + 0.436a_{t-14} + 0.410a_{t-15} + 0.308a_{t-16}),$$

i.e., catch this month is equal to the catch during the same month last year, adjusted by a difference of the weighted sums of the forecasting errors over the previous 4 mo. If the forecasts this year have consistently underpredicted compared with last year's forecasts, then the estimated catch is increased, while if the forecasts this year have consistently overpredicted compared with last year's forecasts, then the estimated catch is decreased. The forecast maintains a balance between keeping the catch in equilibrium and keeping the error in equilibrium.

This impression of a yearly cycle with variability is reinforced when examining the polynomial

TABLE 9.—Estimated cross-correlation function, impulse response function, and noise autocovariance function for a catch-effort transfer model for the Hawaii skipjack tuna fleet, 1964-78.

Lag (mo)	Estimated cross-correlation	Estimated noise autocovariance	SE	Estimated impulse response weights
0	0.651	—		8.409
1	.080	0.49	0.10	1.035
2	.070	.21	.12	.903
3	.086	.16	.12	1.111
4	−.033	.16	.13	−.431
5	.044	.10	.13	.566
6	−.098	.07	.13	−1.269
7	.099	.03	.13	1.276
8	.103	.13	.13	1.334
9	−.017	.14	.13	−.215
10	.043	−.05	.13	.556
11	−.040	−.14	.13	−.517
12	−.20	−.26	.13	−1.555
13	.026	−.05	.14	.338
14	−.109	.05	.14	−1.404
15	.003	−.12	.14	− 038
16	−.098	−.16	.14	−.415
17	.014	−.01	.14	.043
18	−.110	−.05	.14	−1.271
19	− 037	−.12	.14	.185
20	.006	−.12	.14	−1.422
21	−.006	−.16	14	−.475
22	−.108	−.11	.14	.080
23	.012	−.18	.15	−.075
24	− 108	− 21	.15	−1.393
25	−.001	−.09	.15	.181
26	−.108	−.08	.15	−1.390

TABLE 10.—Parameter estimates for transfer model, Model (4) (see text). (Based on 180 observations.)

Parameter	Estimate suppressing backforecasting	SE	Estimate using backforecasting	SE
ω_0	7.5989	0.69403	8.0003	0.83561
θ_1	− 47621	07993	− 48894	.07851
θ_2	−.32874	.08734	−.32633	08541
θ_3	−.17034	08803	− 14853	.08666
θ_4	−.20033	07905	−.17506	.07822
Θ_1	83384	05271	99587	.00707
χ^2 statistic on residuals	34 953 with 43 df		32.018 with 43 df	
Residual mean square	83,323		71,300	
Residual SE	288.66		267.02	
Residual mean	−15.152		0.18650	

TABLE 11.—Parameter estimates for transfer model, Model (5) (see text). (Based on 180 observations.)

Parameter	Estimate suppressing backforecasting	SE	Estimate using backforecasting	SE
δ_1	0.01286	0.30389	0.86672	0.22308
δ_2	.88121	.28641	−.70763	.21659
ω_0	7.3488	.73352	8.1855	.82832
ω_1	−1.3011	2.16847	6.7421	1.71214
ω_2	6.8509	2.34577	−7.3133	1.58459
θ_1	−.49924	.08302	−.46980	.08013
θ_2	−.29495	.09102	− 33234	.08870
θ_3	−.16384	.09191	−.17199	.09012
θ_4	−.13639	.08352	−.21746	.08098
Θ_1	.83311	.05511	.99543	.00623
χ^2 statistic on residuals	33 067 with 43 df		38.906 with 43 df	
Residual mean square	85,673		69,066	
Residual SE	292.70		262.80	
Residual mean	−1.9979		−2.4666	

TABLE 12.—Catch forecasts for 1979 for the Hawaii skipjack tuna fleet from Models (1), (4), and (5) (see text).

Month	Model			Observed catch
	(4)	(5)	(1)	
Jan.	102.24	157.48	159.97	52.6488
Feb.	78.91	123.32	117.81	74.1184
Mar.	121.86	118.83	108.40	102.4088
Apr.	202.05	169.75	175.82	131 0658
May	423.40	406.87	423.95	470.5450
June	595.39	605.68	598.17	358.5100
July	666.16	684.99	607.07	600.6930
Aug.	528.09	535.73	523.14	600.5200
Sept.	297.96	294.92	291.97	148.3070
Oct.	224.28	216.64	222.96	79.3360
Nov.	173.99	168.83	172.94	27.5084
Dec.	133.22	131.61	132.58	84.7755
Total	3,547.55	3,614.65	3,534.78	2.730.4367

TABLE 13.—Predicted and observed number of fishing trips for the Hawaii skipjack tuna fleet in 1979.

Month	Original prediction	Updated prediction	Observed
Jan.	98.93		53
Feb.	97.50		75
Mar.	101.06		78
Apr.	122.30		118
May	174.00	167.71	173
June	196.16	187.36	182
July	209.37	206.14	200
Aug.	183.04	179.81	174
Sept.	139.18	138.73	84
Oct.	121.20	120.45	84
Nov.	104.23	104.83	51
Dec.	100.92	100.51	109

TABLE 14.—Updated forecasts of total catch for 1979 for the Hawaii skipjack tuna fleet.

Month	Model			Observed catch
	(4)	(5)	(1)	
May	393.214	382.430	401.874	470.545
June	547.014	586.400	589.524	358.510
July	644.638	705.137	668.895	600.693
Aug.	500.151	527.945	521 456	600.520
Sept.	293.130	283.067	289.516	148 307
Oct.	220.557	197.953	222.806	79.336
Nov.	174.567	164.720	173.594	27 5084
Dec.	130.947	136.831	133.148	84 7755
Total	2,904.218	2,984 483	3.000.813	2.370 1949

representation of Model (1). The value of Θ_1 is nearly one. Thus the term $(1 - B^{12})$ appears on both sides of the equation, and can be cancelled. Abraham and Box (1978) showed that this is sufficient reason to suspect a deterministic cosine function trend with a moving average model around the trend. Given the high residual mean square for the model (115, 170), this latter interpretation is consistent with the folklore on the fishery—highly variable but on the average things are similar from year to year.

The first transfer function model is:

$$y_t = 8.003x_t + (y_{t-12} - 8.003x_{t-12}) + (a_t + 0.489a_{t-1} + 0.326a_{t-2} + 0.149a_{t-3} + 0.175a_{t-4}) \qquad (7)$$

$$- (0.996a_{t-12} + 0.487a_{t-13} + 0.325a_{t-14} + 0.148a_{t-15} + 0.174a_{t-16}).$$

This model has an interpretation similar to that of the univariate model, except now catch per weighted units of effort are compared between years. The second transfer function model compares lagged values of catch and effort also.

It is difficult to judge the value of a forecast, since this will depend on the use being made of the forecast and the alternatives available. Granger and Newbold (1977) suggested the most appropriate measure of the value of a forecast is a loss function which reflects the loss from inaccurate forecast in the actual application for which the forecasts were developed. For forecasting the skipjack tuna fishery in Hawaii, there were four immediate goals. The first was to give a reasonably accurate estimate of total catch over the year, within a 15-20% error rate. The second was to predict what kind of summer it would be, May through September being the main fishing months. This means predicting what month the fish start running, what month the fish stop running, and whether the catch is high and peaked as in 1979, or flat and low as in 1978. An important concern is the relative size of the drop in catch when it occurs in September or October.

A third concern was an accurate forecast of the catch in December, when the holiday demand for sashimi (a Japanese raw fish delicacy) drives prices very high. And finally, an increased understanding of the dynamics of the fishery was desired.

Based on these criteria, I feel the forecasts have performed well, especially compared with any alternative available. The error in predicting the 1979 total catch is higher than desired. However, for the last 6 mo of 1977 the model forecasted within 8% of the observed total catch, and for the period July 1977-December 1978 the model forecasted within 12% of the observed total catch.

Except for June 1979, the summer months were predicted accurately. Experience with the model on the data from July 1977 suggests that the summer months are almost always predicted within 10% of the observed catch. In fact, in March 1979, an industry representative doubted the high catch forecasted for the summer, due to the low catch in January and February 1979. Similarly, the sharp drop in catch in September was predicted by the model. Again, in August 1979 an industry representative doubted that a sharp decline in catch would occur in September, but said that this could be a useful piece of knowledge since their decisions would change if they knew they could expect the supply to drop sharply.

The forecasts have provided insight into the fishery. The major failures of the forecasts were January 1979 and October-December 1979. January 1979 was a period of unusually bad storms, so that few fishing trips were made. However, the observed catch per trip was 0.993 metric tons (t), while Model (4) predicted a catch per trip of 1.033 t. The main source of the error in the forecast was the predicted number of trips to be made.

Similarly, the high summer catches, coupled with very high catches of yellowfin tuna, drove the price for skipjack tuna to very low levels. At the end of September, most of the boats went into drydock because of the prevailing low prices. The few boats that remained tended not to be the industry leaders (i.e., boats with a proven record of higher catch rates), and made only short forays rather than their usual fishing trips.

The point of these explanations is that the causes of the poor forecasts appear to be related not to the behavior of the fish stocks but rather to the behavior of the fishermen. Therefore, the effort to improve the forecasts needs to be directed at understanding the fishery, rather than the fish. (An economic study of the industry is near completion.)

Finally, water temperature and salinity data for one location off Oahu were included in the transfer function models. These variables added little to the forecasts, and since there is no mechanistic explanation as to why these variables should affect the catch and effort, they are not being used at this time in the forecasts. (However, the ability to include random environmental factors into the forecasting model is an advantage when using stochastic models as compared with the normal deterministic production models.) Disaggregating by size class might also improve the forecasts. Prior to 1973, the catch of the large skipjack tuna and the total catch were highly correlated. Since 1973, this has not been true and there has been a definite change in the size composition of the catch. A disaggregated intervention model may be able to explain this change.

SUMMARY

Box-Jenkins models have been proposed as an alternate model for forecasting fishery data. ARIMA models provide maximum likelihood estimators that are not biased when the data is seasonal and autocorrelated, and when a variable is lagged on itself. Techniques are explored which allow the model to be constructed from the data up, rather than from theoretical models that may not be supported by the data. The procedure is illustrated on skipjack tuna catches in Hawaii, which traditionally has been considered too variable to forecast on a monthly basis in a reasonable manner.

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SPATIAL COVARIATION OF DAILY GROWTH RATES OF LARVAL NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, AND NORTHERN LAMPFISH, *STENOBRACHIUS LEUCOPSARUS*

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The widths of the outer three daily growth increments in the otoliths of larval *Engraulis mordax* (Engraulidae) and *Stenobrachius leucopsarus* (Myctophidae) were used as a measure of recent growth rate. From 10 samples collected off the coast of Oregon, 367 *E. mordax* and 141 *S. leucopsarus* individuals were analyzed. The overall mean growth rate of *S. leucopsarus* increased from 0.11 mm per day at a length of 5 mm to 0.28 mm per day at 15 mm. For *E. mordax*, growth rate declined from 0.57 per day at 5 mm to 0.41 mm per day at 15 mm. Within-and between-sample variance in growth rate was small, no spatial trends were detected. Correlations between *E. mordax* growth rate and *S. leucopsarus* growth rate among the 10 samples were not significant.

INTRODUCTION

The growth rate of young fish varies greatly in response to temperature and ration (Brett, 1979) and can be accurately measured in wild fish by analyzing daily growth increments in otoliths (Brothers et al., 1976; Struhsaker and Uchiyama, 1976; Methot and Kramer, 1979). After correcting for the effect of temperature on growth, the mean growth rate of larval fish in the sea is an indicator of the degree to which growth, and presumably survival, of larval fish is food limited. Variability in growth and condition provides information on time and space scales of ecologically important patchiness in the sea. Anchovy larvae show evidence of variation in growth rate (Methot and Kramer, 1979) and starvation indices (O'Connell, 1980) on scales of 1–100 km while 1–10 m patches of prey can be vital for successful first feeding by anchovy larvae (Lasker, 1975). When variability in larval growth rate of two or more species is compared, one may obtain information on the environmental variables which influence growth and survival of larval fish. Significant positive correlations in growth rate between species, i.e., similar spatial-temporal patterns of deviations from their respective mean growth rates, may indicate that these species respond to some set of environmental variables in the same way. Significant negative correlations suggest that responses to environmental conditions differ between the species. Nonsignificant correlations may mean that growth of each species is limited by different, specific environmental factors and these factors tend not to covary on scales larger than the scale of the sampler. The object of this study is a comparison of the growth rates of northern anchovy, *Engraulis mordax* (Engraulidae), and northern lampfish *Stenobrachius leucopsarus* (Myctophidae), within a specified portion of their distribution. Mean growth rates obtained from this analysis will be the first measure of growth for larval *S. leucopsarus* and for the northern population of *E. mordax*. Covariance in growth rate between species among samples will be examined for clues to relationships between larval fish and their environment.

During the summer along the coast of Oregon, larvae of *E. mordax* and *S. leucopsarus* are the most abundant species in the offshore assemblage of larval fish (Richardson and Pearcy, 1977). Both species inhabit the upper tens of meters of the water column (Ahlstrom, 1959; Richardson and Pearcy, 1977; Fast, 1960). The optimum environmental conditions for the two species may differ for several reasons. Oregon is the center of range for the northernmost of three *E. mordax* populations (Vrooman and Smith, 1971) but is in the south central part of the range of *S. leucopsarus* (Paxton, 1967). July is a prime spawning month for *E. mordax* but is near the end of a protracted spawning season for *S. leucopsarus* (Richardson and Pearcy, 1977). *S. leucopsarus* larvae have a larger mouth and will be able to eat prey unavailable to similar length *E. mordax*.

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Although good estimates of growth rate have been made by examining the relationship between size at capture and number of daily growth increments in otoliths (Brothers et al., 1976; Struhsaker and Uchiyama, 1976; Taubert and Coble, 1977; Methot and Kramer, 1979), this technique has two limitations. Data on size at age integrates growth rate over the lifetime of each larva and may have little meaning for studying environmental effects because environmental conditions are typically measured only at the time of capture. Second, the otolith morphology of larger larvae such as *S. leucopsarus*, obscures the inner increments. Ages cannot be estimated unless one resorts to the tedious procedure of grinding thin sections of the otoliths. Both problems are solved by using the widths of the outer few increments to measure growth rate a few days before capture. This technique requires the additional assumption that otolith growth mirrors fish growth on a day to day basis. Although this assumption has not been rigorously evaluated, Taubert and Coble (1977) found that otolith size was more closely related to fish size than to age. Correspondence between otolith growth and fish growth is routinely assumed in back calculation of size at age from annual marks in otoliths (Ricker, 1969).

METHODS

The NOAA fisheries RV "David Starr Jordan" surveyed along seven transects off the coast of Oregon 19–26 July 1977. Transects extended from the 50 fathom depth contour to a point 90 miles due west. Direction of survey alternated between transects. During the day the distribution of near surface sonar targets, presumably anchovy schools, along one transect was mapped (Hewitt et al., 1976). During the night, two stations were occupied in regions along the transect with high target density. Each station consisted of a CTD cast, plankton sample, nekton sample, followed by a second plankton sample. Plankton samples were oblique tows from 70 m to the surface using a Bongo net with 60 cm mouth diameters, 0.505 mm mesh on one side and 0.333 mm mesh on the other. The 0.505 mm mesh sample was preserved in formalin and the 0.333 mm mesh sample used for otolith studies was preserved in 80% ethanol. The ethanol was changed within 24 h after initial preservation. All fish eggs and larvae were sorted from the ethanol preserved samples. Size distributions were determined from a subsample containing no more than 150 larvae per species. Larvae less than 5 mm were excluded from subsamples used for otolith analysis. Otoliths were dissected out and prepared for viewing according to Methot and Kramer (1979).

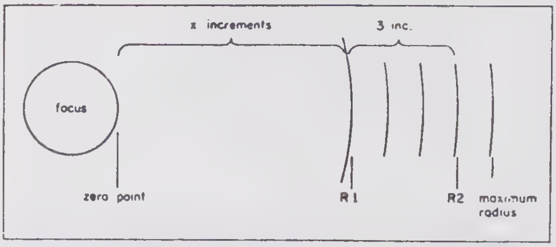

Figure 1. Otolith measurements used to determine otolith size and widths of the outer three complete increments.

Otolith images were viewed on a high resolution TV screen under magnification of 1,500 ×. Total otolith size and width of the outer three complete increments were measured by digitizing the positions of the four points shown in Figure 1 using an electronic cursor (precision ±0.15 μm) and a micro-computer to process the data. All measurements were made along the longest radius of the sagittae (largest otoliths). The data from both otoliths and up to three transects per otolith were combined.

The preserved lengths of *E. mordax* were corrected to live lengths, assuming 5 min elapsed time between capture and fixation (Theilacker, MS). This correction of about 0.8 mm enabled comparisons to other growth studies. No shrinkage correction was applied to the lengths of *S. leucopsarus* larvae.

RESULTS

The distributions of *Engraulis mordax* eggs and larvae and *Stenobrachius leucopsarus* larvae suggest that one mesoscale patch was sampled (Fig. 2a, b, c). Both species occurred in all samples taken at over 15° C and no fish eggs or larvae were found in the colder water nearshore south of 45° N latitude.

Engraulis mordax eggs were most abundant off the mouth of the Columbia River and were not found south of 45° N. Among the 12 positive samples taken north of 45° N the range in mean length was 3.5–7.1 mm for *E. mordax* and 5.1–8.4 mm for *S. leucopsarus*. South of 45° N the range in mean length of *E. mordax* increased to 10.7–14.1 mm and no larvae less than 5 mm were collected; mean lengths of *S. leucopsarus* increased slightly to 8.4–10.0 mm.

Three steps were necessary to convert recent rate of change in otolith size (outer three complete daily growth increments) to range of change in fish length:

1) Define the relation between fish length and otolith radius. Principal component analysis was used rather

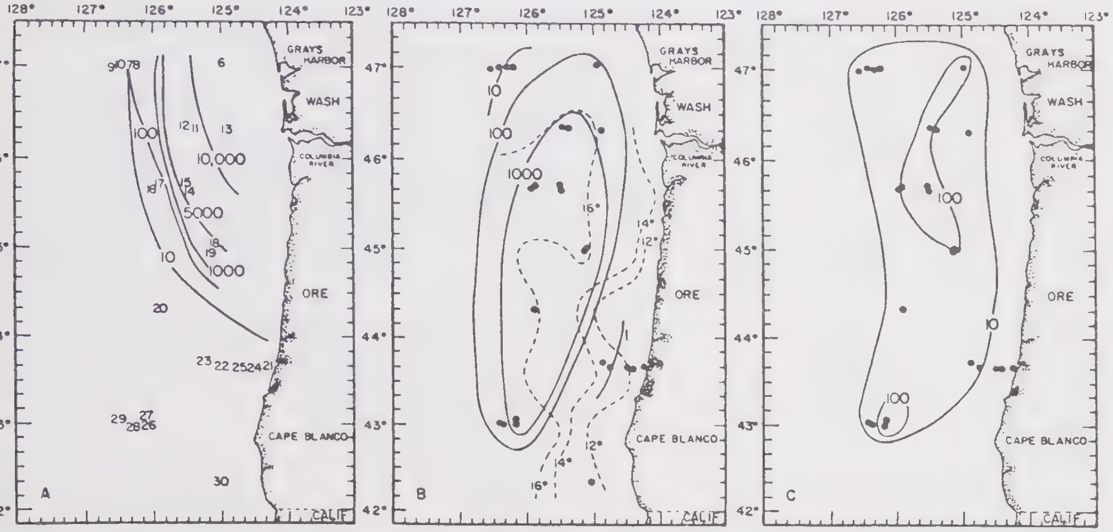

Figure 2. (A) Positions of Bongo samples (number indicates order occupied) and abundance of *Engraulis mordax* eggs (numbers per 10 m^2). (B) Abundance of *Engraulis mordax* larvae (numbers per 10 m^2) and three surface isotherms (dashed line). (C) Abundance of *Stenobrachius leucopsarus* larvae (numbers per 10 m^2).

than linear regression (Harris, 1975; Ricker, 1973) because variable shrinkage and difficulty in measuring bent or decomposing specimens could have introduced over 0.5 mm error in the measurement of fish length.

2) Multiply the two otolith measurements, R1 and R2, (Fig. 1) by the ratio: expected otolith radius/measured otolith meaximum radius. This corrects for the expectation of larger (smaller) increments in otoliths of larvae with larger (smaller) than expected otolith size.

3) Convert the adjusted otolith measurements to estimates of fish length using the principal axis defined in step one above. The assumptions inherent to this technique are discussed below.

The relation between maximum radius and standard length was linear for *S. leucopsarus* and nonlinear for *E. mordax* (Fig. 3). The data for *E. mordax* were linearized by taking the logarithm of both variables. The relationship between the variables was defined by principal component analysis after converting standard length and radius measurements to standard deviation units (Table 1).

For each specimen a first principal component score was calculated from standardized measurements of standard length and otolith radius then used to calculate a predicted otolith radius. Data from a specimen were not used if the ratio of predicted otolith radius to measured otolith radius was greater than 1.25 or less than 0.8. By this criterion 1 *E. mordax* and

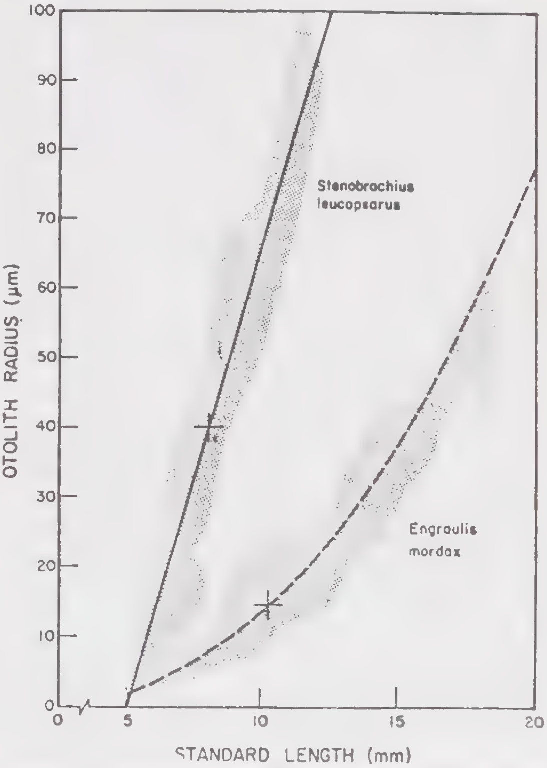

Figure 3. Relationship between maximum radius of otolith and length of larva. Stipled areas are the range of the data.

Table 1. First principal component of standard length and otolith radius. Variables were converted to normal deviations before analysis.

		Standard length		Otolith radius		Percent variance in 1st principal
		Mean	Variance	Mean	Variance	component
Engraulis mordax	linear	10.76	10.08	18.64	169.43	97.2
	log-log	2.335	0.0921	2.672	0.5959	98.2
Stenobrachius leucopsarus	linear	9.12	4.57	39.83	782.28	99.8

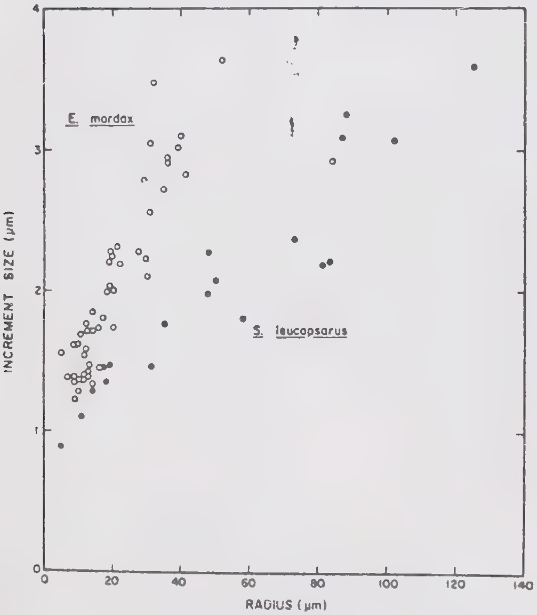

Figure 4. Distribution of mean size of the outer three complete increments with respect to the radial distance to the midpoint of these three increments. Increment size is otolith growth rate in µm per day. Data are from sample 27.

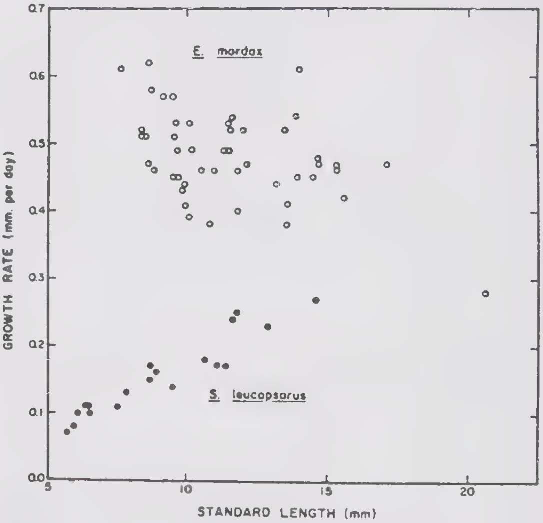

Figure 5. Same data as in Figure 4 but otolith measurements were transformed to fish lengths.

32 *S. leucopsarus* were not considered in the growth rate analysis. The two otolith measurements, R1 and R2, were multiplied by this ratio.

Mean increment size (R1-R2)/3, is presented as a function of radius to the center of the measurement interval, (R1+R2)/2, for one sample in Figure 4. Otolith growth is faster in larger specimens of both species. When these same data are transformed from otolith size to fish length the pattern of growth with respect to size differs between the two species (Fig. 5). Wider increments deposited by larger *E. mordax* did not necessarily reflect increased fish growth rate because of the non-linear relation between otolith size and fish length. In other samples the same trends were apparent (Table 2). *E. mordax* grew 2–3 times faster than *S. leucopsarus*. Large *S. leucopsarus* grew faster than small *S. leucopsarus*. Large *E. mordax* grew at the same rate or slightly slower than small individuals.

These data on size-specific growth rates were summarized into a single indicator of the quality of each species environment at each sample site by calculating the linear, least-squares regression of growth rate on size (Table 2) then using these equations to estimate growth rates at the overall mean lengths analyzed (10 mm for *E. mordax* and 8.5 mm for *S. leucopsarus*) (Fig. 6). The error bars shown in Figure 6 are not sufficiently conservative because they do not account for error in the adjustment ratios applied to the data, but the high incidence of non-overlap does suggest some significant between-sample variation in growth rate. However, the absolute magnitudes of the deviations (Fig. 6) were small compared to the scope for growth in anchovy larvae (Fig. 7), the two members of a pair of samples were often dissimilar in growth (compare samples 26 and 27 in Fig. 6), and correlation between growth rate of *E. mordax* and *S.*

Table 2. Relationship between growth rate (mm per day) and length of larva (mm) in each sample.

	Engraulis mordax					*Stenobrachius leucopsarus*				
Sample	N	Mean length	Slope	Intercept	Standard error (reg)	N	Mean length	Slope	Intercept	Standard error (reg)
6	5	8.1	−0.0324	0.707	0.090					
11	22	7.3	−0.0252	0.690	0.102	6	6.0	0.0072	0.075	0.021
12	14	8.3	−0.0282	0.753	0.088	11	6.3	0.0030	0.129	0.029
13	7	7.0	−0.0474	0.898	0.031					
14	26	9.2	−0.0256	0.745	0.072	13	8.1	0.0151	0.083	0.048
15	29	9.2	−0.0297	0.729	0.075	20	7.0	0.0328	−0.075	0.036
16	27	8.3	−0.0200	0.681	0.066	19	8.6	0.0239	−0.031	0.020
17	39	8.6	−0.0212	0.735	0.075	6	8.1	0.0144	0.021	0.018
18	30	7.0	−0.0236	0.684	0.080					
26	49	12.4	−0.0060	0.490	0.059	33	9.4	0.0165	0.022	0.026
27	49	11.5	−0.0137	0.644	0.067	19	9.1	0.0207	−0.032	0.020
28	47	12.3	−0.0109	0.607	0.071	3	10.3	0.0418	−0.246	0.024
29	23	12.7	−0.0049	0.497	0.062	9	10.3	0.0310	−0.065	0.065
Combined	367	10.0	−0.0167	0.654	0.078	141	8.4	0.0185	0.016	0.039

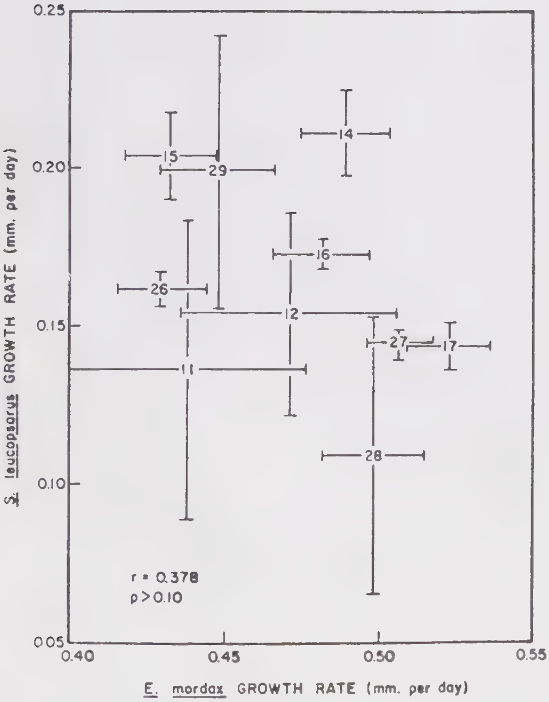

Figure 6. Growth rates of *E. mordax* (mm per day at 10 mm) and *S. leucopsarus* (mm per day at 8.5 mm) estimated from the regression equations in Table 2. Plotted points are the sample numbers (see Fig. 2A). Error bars are ±1 standard error. Correlation between growth rate of *E. mordax* and growth rate of *S. leucopsarus* was not significant.

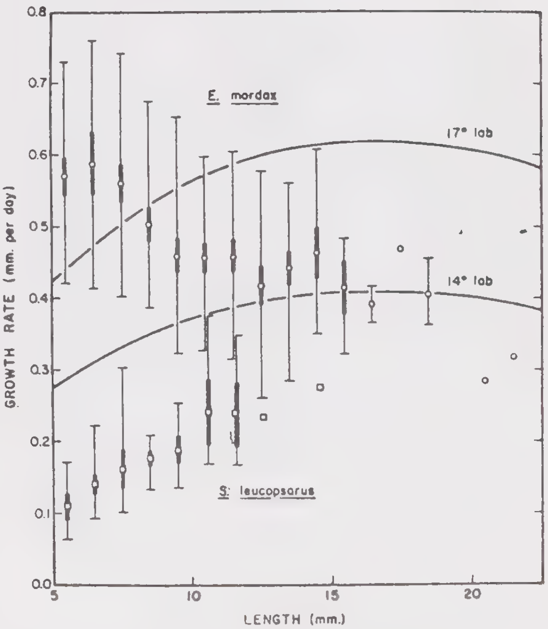

Figure 7. Distribution of growth rate (heavy vertical bars are ±2 standard errors, narrow vertical bars are the range) in each 1 mm size interval. Data from all samples combined. Also shown are the relationships between daily growth rate and size at two temperatures in the laboratory (derived from model in Zweifel and Hunter, pers. comm.).

leucopsarus among these 10 samples was not significant. Since some of the regression equations in Table 2 were not significant the estimates of growth rate at a standard size were also calculated using the mean growth rate for each species in each sample and a relation between growth and size derived from all data for that species. This shifted the points displayed in Fig. 6 by an amount less than the standard errors shown in that figure. The correlation in growth rate between the two species was still not significant.

ASSUMPTIONS

1) One growth unit is deposited per day. This was confirmed for *E. mordax* using laboratory-reared larvae (Brothers et al., 1976). No confirmation is available for *S. leucopsarus* but the growth units appeared similar to those in *E. mordax* and other species examined in the laboratory. Sub-daily growth increments were occasionally observed in both species and distinguished from the daily growth units (Taubert and Coble, 1977).

2) Otolith increment size is a function of growth rate. This relation is assumed from the close correlation between otolith size and fish size.

3) Outer increment size should be adjusted by the ratio, expected otolith size/measured otolith size, before interpreting increment size as an absolute measure of growth rate. This assumes that this ratio was constant over the lifetime of the larva. The method of calculating expected otolith size was critical. When calculated from a linear regression of otolith radius on fish length the resulting adjustment ratio tended to over-correct the otolith measurements. Recognizing that mismeasurement of fish length was not trivial, the relation between otolith radius and fish length was defined by principal component analysis. This resulted in an expected otolith size that was a function of measured otolith size as well as fish length. The bias introduced by mismeasured fish was reduced. For larvae with otolith radii less than about 10 μm, error in measuring otolith radius also introduced some error in the adjustment ratio.

DISCUSSION

Within the region sampled, *Engraulis mordax* and *Stenobrachius leucopsarus* larvae were abundant and had similar distributions (Fig. 2b, c). Each species showed little variation in growth rate and the null hypothesis, no correlation in growth rate between species could not rejected. However, the null hypothesis certainly cannot be accepted until samples from a larger domain of environmental conditions with greater range in growth rate are examined. In this study, the surface temperature ranged less than 1° C in the set of 13 samples analyzed and the sample mean growth rates of 10 mm *E. mordax* ranged from 0.42 to 0.52 mm per day. A wider range, 0.34–0.55 mm per day, was found among 12 samples in the more heterogeneous waters off southern California (Methot and Kramer, 1979). In the laboratory the range of growth rates obtained when temperature and ration are manipulated is greater than 0.5 mm per day (several experiments are summarized in Methot and Kramer, 1979).

These data are the first estimates of growth rate for larval *Stenobrachius leucopsarus* and for the northern population of *Engraulis mordax*. The mean growth rate of *S. leucopsarus* larvae increased from 0.11 mm per day at 5 mm to 0.28 mm per day at 15 mm (Fig. 7). *E. mordax* larvae grew more rapidly (0.57 mm per day at 5 mm to 0.41 mm per day at 15 mm).

Although ages of individual larvae usually were not determined, the distributions of size at age were estimated by simulating growth curves using distributions of growth rate in each 1 mm size category (Fig. 7). In these simulations age 0 was defined as the onset of daily otolith increment formation (approximately at completion of yolk absorption, 5 days past hatch in *E. mordax*) and size at age 0 was 4.2 mm in *E. mordax* and 4.5 mm in *S. leucopsarus*. Simulations were run using the mean, minimum, maximum and ±2 standard errors of growth rate in each 1 mm size category (Fig. 8). Methot and Kramer (1979) determined growth rates of *E. mordax* by counting daily growth increments. Within samples, larvae 15 days old typically had a 3 mm range in size. In the present study, using data from all samples, simulated size at age 15 days had a range of 4 mm.

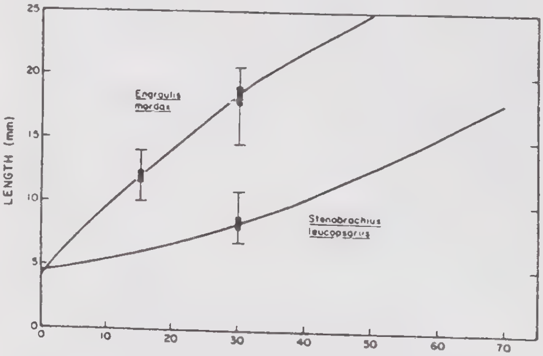

Figure 8. Simulation of size at age using size specific growth rate data in Figure 7. Trajectories are the result when mean growth rate in each 1 mm size category is used. Wide vertical bars show range of size at age with ±2 standard errors of growth rate and narrow vertical bars show range with minimum and maximum growth rates.

Thus, growth rates from widths of outer increments seem as precise as those obtained from a trend of size at age. For *S. leucopsarus* it was not possible to count the total number of increments, consequently the outer increment method was invaluable.

Although *E. mordax* larvae were growing 2–3 times faster than *S. leucopsarus* larvae on the basis of length, their growth rates may be nearly the same on a weight basis. Unfortunately, the appropriate length-weight conversions are not available. Using the length-dry weight relation of Hunter (1976) for laboratory reared *E. mordax* larvae and extrapolating the length-dry weight relation for juvenile and adult *S. leucopsarus* of Smoker and Pearcy (1970), I estimated that 10–20 mm *S. leucopsarus* are 3.5–4.0 times heavier than *E. mordax* in the same size range. This approximately offsets the difference in growth based on length. In the future more precise estimates of weight should be made so we can compare the absolute growth rates of various larval fish species.

No other estimates of the growth rate of larval *Stenobrachius leucopsarus* are available. Larvae in the 5–15 mm size range are found for several months (Fast, 1960; Richardson and Pearcy, 1977) so modal progressions cannot be used to estimate growth rates. Smoker and Pearcy (1970) found recruitment of juveniles into the 20–25 mm size class beginning in August–October. If the 10 mm larvae collected in this study continued growing at 0.2 mm per day they would be in the 20–25 mm size range in September.

Mean growth rates of *E. mordax* larvae in the 8–12 mm size range were 0.52–0.45 mm per day and the mean surface temperature at which specimens were collected was 16.1° C. Larvae in the same size range in a laboratory rearing experiment at 16.2° C (Hunter, 1976) were growing 0.54–0.60 mm per day. In general, larvae larger than 8 mm were growing at the same rates as larvae reared in the laboratory at about 15° C (curves in Fig. 8 were derived from parameters of a growth model prepared by Zweifel and Hunter, pers. comm.). Although the growth rates of 5–8 mm larvae may have been over-estimated they still are within reasonable limits; similar to the growth of 5–8 mm larvae at 18° C in the laboratory. Considering the uncertain relation between surface temperature and the temperature experienced by the larvae, these data support the general conclusion of Methot and Kramer (1979) that growth of anchovy larvae is similar in the laboratory and in the sea.

SUMMARY

1) Larvae of northern anchovy, *Engraulis mordax*, and northern lampfish, *Stenobrachius leucopsarus*, were abundant off the coast of Oregon in July 1977. Both occurred in all samples taken at 15° C or warmer.

2) The growth rates of 367 *Engraulis mordax* and 141 *Stenobrachius leucopsarus* were determined by measuring the widths of recent daily growth increments of otoliths.

3) Very little variation in growth rate was observed between samples and the correlation in growth rate between species was not significant.

4) The mean growth rate of *Stenobrachius leucopsarus* increased from 0.11 mm per day at a size of 5 mm to 0.28 mm per day at 15 mm. This is the first growth rate estimate for larvae of this species.

5) The mean growth rate of *Engraulis mordax* larvae declined from 0.57 mm per day at 5 mm to 0.41 mm per day at 15 mm. This is very similar to the growth rate of anchovy reared in the laboratory at similar temperatures (15°–16.3° C).

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VARIATION OF THE PACIFIC NORTH EQUATORIAL COUNTERCURRENT OBSERVED BY SHIPS-OF-OPPORTUNITY

by

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Approximately 17 merchant vessels were used during 1979 to monitor the tropical Pacific subsurface temperature by expendable bathythermograph (XBT). The ships' routes are shown in Figure 1. The number of equatorial crossings on each route is indicated within parentheses. The supporting institutions and responsible oceanographers are given in Table 1. Baroclinic structure observed by these ships in the vicinity of the Pacific North Equatorial Countercurrent is discussed in this paper. One ship provided approximately bi-monthly sections across the current in the western Pacific on the route between Noumea and Japan. Nine ships provided approximately weekly sections across the current in the central Pacific south of Hawaii. The temporal evolution in strength of the Countercurrent is described in this paper and its variability in the western and central Pacific is compared.

TABLE 1

ROUTE	INSTITUTION	OCEANOGRAPHER IN CHARGE
New Caledonia/Tahiti to Hong Kong/Japan/Panama California	ORSTOM-Noumea	J. R. Donguy
Australia/New Zealand to U.S. West Coast	FNOC-Monterey	P. Stevens
Australia/Samoa/Tahiti to U.S. West Coast	NOAA-Monterey*	D. McLain

Table 1. Institutions and oceanographers in charge of the merchant ships taking XBT observations on routes shown in Figure 1.

* Scripps Institution of Oceanography since 1980.

WESTERN PACIFIC - NOUMEA/JAPAN SECTION

Sixteen meridional temperature sections were obtained by the merchant vessel Hachiyo Maru near 157°E from June 1979 to May 1980. Four sections (Fig. 2) show the major changes in baroclinic structure observed during the year. The North Equatorial Countercurrent appears in these sections between a trough in the thermocline topography near 3°N and a ridge near 8°N. The trough and ridge are weakly developed in the section of 27 July - 2 August 1979 and strongly developed in the section of 8-16 February 1980. The latitude of each XBT drop is marked at the bottom of each section and shows that the typical spacing between drops is approximately 1 latitude.

The strength of the Countercurrent was monitored by the meridional slope of the 20°C isotherm between the trough and ridge, using a simple two-layer approximation (Wyrtki and Kendall, 1967). The depth of this isotherm at the ridge (D_n) or trough (D_s) was determined from the 16 temperature sections, as well as the mean depth $\overline{D}$ and the difference $\triangle D$ (Fig. 3). A low frequency signal has been observed by the Hachiyo Maru in spite of the data gap from December to February. Depth at the trough and ridge vary almost exactly out of phase, while the mean depth remains nearly constant. The current strength as indicated by $\triangle D$ varied from weak during June-July 1979 to strong during December-February 1979/80, then weak again during April-June 1980.

Although the South Equatorial Countercurrent (5°-10°S) is beyond the scope of this study, it is interesting to contrast it with its northern counterpart. The eastward contercurrent shear in the southern hemisphere appears distinctly in the thermocline above 20°C (Fig. 2), while in the northern hemisphere the shear involves virtually all the main thermocline down to 11°C. The southern current strengthens after February while the northern current weakens.

CENTRAL PACIFIC
AUSTRALIA (VICINITY) TO U.S. WEST COAST

The same technique was used to analyze 35 temperature sections obtained by 9 ships in the central Pacific between January 1979 and April 1980. The index ($\triangle D$) of Countercurrent strength indicates a weak current during April-June 1979, followed by a strong current during September-December, then weak again after March, 1980 (Fig. 4). It is remarkable that there is almost no difference in phase of Countercurrent strength between the central and western Pacific. The west appears to lag by 1 or 2 months, but this difference may not be significant due to the poorly resolved peak in the west and the large scatter of values near the peak in the central region. Note that the central Pacific sections are taken over a wide band of longitude from 130°W to 170°w (Fig. 4, bottom). The mean east/west slope of the thermocline during 1979/80 was used to project all the estimates to 155 W. This projection alters D_n and D_s by 1 to 20 m but does not change the estimate of $\triangle D$.

Temperature sections taken by merchant vessels have the deficiency that XBT drops are taken at someshat irregular intervals. The number of drops per day ranges from 2-6, depending on the agreement between ships' officers and the oceanographer in charge. The central Pacific sections were divided into two groups having a latitude spacing of approximately 1° - or 2° - latitude, and plotted in Fig. 4 with different symbols. Nearly half of the sections have 2° spacing, which does not always adequately resolve the Countercurrent. These sections give a slightly smaller estimate of Countercurrent strength than the sections with 1° - spacing during the time of peak strength from October to December, because the thermocline ridge or trough falls between drops.

COMPARISON TO HAWAII/TAHITI SHUTTLE

Temperature sections across the Countercurrent at approximately weekly intervals were obtained near 155°W by research vessels and aircraft during the Hawaii/Tahiti Shuttle Experiment. Preliminary results have been described in a recent article by Wyrtki et al (1981). The index of Countercurrent strength $\triangle D$ averaged monthly from the Shuttle observations is compared to the similar index from ships-of-opportunity in Fig. 5. A number in parenthesis by each plotted point indicates the month of 1979 for the averaged values. The monthly averages of Shuttle and ship-of-opportunity observations are highly correlated (0.94). A comparison of individual ship-of-opportunity sections to weekly averages of the Shuttle data (not presented) was also highly correlated (0.81). The high correlation clearly is due to the regular annual signal (Meyers, 1975, 1979) in both data sets. Past studies have shown that interannual fluctuations in the equatorial current system (Wyrtki, 1978, 1979; Donguy and Henin, 1981) are generally more energetic than the annual signal. The RMS deviation between monthly averaged $\triangle D$ from Shuttle and ship-of-opportunity observations is small error increases our confidence that XBT ships-of-opportunity can be used to economically monitor both annual and interannual variation in baroclinic structure of the tropical Pacific.

OBJECTIVE ANALYSIS
XBT DATA RECEIVED AT FNOC BY RADIO

Some ($\approx$50%) of the XBT observations from ships-of-opportunity during 1979/80 were sent to FNOC, Monterey by radio on the global telecommunications system. They were merged at Monterey with radio reports from naval and research vessels. A linear, least-squares interpolation scheme (objective analysis) was used to map subsurface temperature throughout the tropical Pacific using the radioed data. Data from the Hawaii/Tahiti Shuttle Experiment were first eliminated and held out as a high quality control case to test the effectiveness of the interpolation scheme and ship-of-opportunity network.

Interpolated results are shown for the temperature anomaly at 160m. The anomaly is the departure from the longterm annual mean temperature. This allows annual variations, if present, to appear in the interpolated data. The mean was estimated from all XBT and MBT observations in the FNOC archives as of 1975, the majortiy of drops taken during 1950 to 1970. After removing the mean from the temperature at 160m for each XBT cast, the sesiduals for each month were interpolated to a 2°-latitude by 10°-longitude grid between 30°N and 20°S, using a Gandin-type objective analysis scheme. The scan dadius for accepting observations at a grid point was ± 15°-longitude, ± 3°-latitude, and ± 0.5 month. The objective analysis was not attempted at grid points with less than 2 observations within the scan radii. The spatial autocorrelation function used was an exponential decay with e-folding length of 1500 km east/west and 500 km north/south. The temporal autocorrelation function was assumed to be unity, which is conservatively small estimate. This permits a considerable amount of smoothing of the data.

TEMPERATURE ANOMALY AT 160 M

The mapped anomaly for each month shows coherence in sign over very large areas (Fig. 6), much larger in fact, than the scan radii. There are two possible explanations for these large scale anomalies. The first possibility is that the mean value used to remove climatology from the observations has a bias of large spatial scale. We do not think this is the case, but it will not be proven until the mapped anomalies show oscillations in sign throughout the region during the course of several years. The second possibility is that the large scale anomalies are truly an indication of ocean variability. This will become more believable as reasonable, physical interpretation of them is achieved.

The preliminary analysis is encouraging. Some of the anomalies evolve slowly in time. For example, variation of the North Equatorial Countercurrent already discussed in the analysis of the temperature sections appears on the maps. The weak current (westward anomaly) in June 1979 (Fig. 6, top) has warm water on its northern side near 10°N, in accordance with the "thermal wind" relation. The strong current (eastward anomaly) in November 1979 (Fig. 6, middle) has warm water on its southern side south of 3° to 7°N. An interesting evolution of the anomaly begins in November 1979, with the warm zone on the equator in the central Pacific near 140°W. An earlier map (not presented) shows it entering the region from the east. Lack of data in the radio reports does not allow connecting it to the region off Central and South America during earlier months, as seen on the June 1979 map. From the Central Pacific this warm zone progresses westward and southward across the equator until it reaches New Guinea in February 1980 (Fig. 6, bottom). We hope that a more complete description of this evolution of the temperature field, particularly in the eastern Pacific, will be possible after all the observations from the ORSTOM, FNOC, and NOAA (PEG) programs, as well as data from the Shuttle and EPOCS programs are merged with the other radio reports.

FUTURE RESEARCH PLANS

Our future research plans are: 1) Make a careful comparison of these preliminary maps with results from the Shuttle, in order to fine-tune the statistical structure used in the interpolation scheme. 2) Map the heat content of 0/400m, sea surface temperature and mixed layer depth throughout the tropical Pacific using the largest possible merger XBT data. 3) Relate the variability to the wind field.

In the longer run, we intend to merge the analysis of the XBT records with sea level records. Historical data indicates that sea level and dynamic height are highly correlated (Fig. 7), at least in the tropical Pacific. Dynamic height in turn can be accurately estimated from the vertical heat integral in this region because of the tight T-S relationship. Ultimately, we hope that this sea level mapping effort can be extended into the realm of smaller, synoptic space and time scales through the inclusion of new observations becoming available in the satellite ara, such as current and temperature monitored with tracked drifters, (Patzert, 1981) and sea level with the satellite altimeter.

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FIGURE CAPTIONS

Figure 1. XBT sections by ships-of-opportunity January 1979 to June 1980. Number of sections obtained given in parentheses (). The start date is indicated on sections which did not begin prior to January 1979. Dashed lines give routes serviced by ORSTOM-Noumea, solid lines routes serviced by FNOC or NOAA, Monterey.

Figure 2. Meridional temperature sections (°C) near 157°E obtained by *Hachiyo Maru* between Noumea, New Caledonia and Japan. Temperature exceeding 29°C is stippled. Latitude of XBT drops indicated by x at bottom.

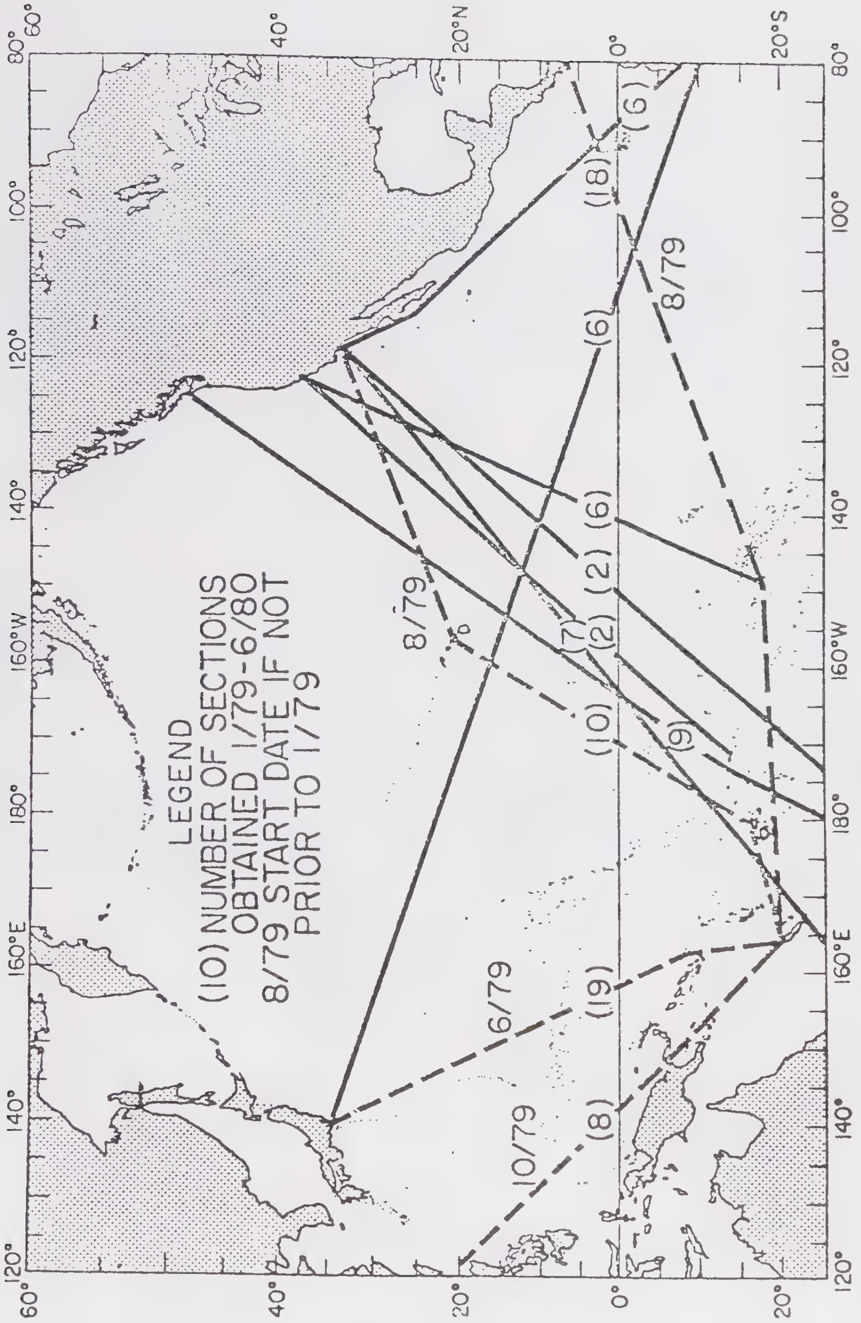
Figure 3. Development of the slope of the 20°C isotherm across the North Equatorial Countercurrent-Western Pacific. The depths of the 20°C isotherm at the northern and southern flanks of the current are indicated by D_n and D_s respectively. The mean depth is $\overline{D}$ and the difference is $\triangle D$. All temperature sections crossed Countercurrent near 157°E.

Figure 4. Same as Fig. 3 - Central Pacific. Temperature sections crossed Countercurrent between 130°-170°W (bottom).

Figure 5. Slope of the 20°C isotherm across the North Equatorial Countercurrent observed by ships-of-opportunity and by research ships and aircraft during the Hawaii-to-Tahiti Shuttle (Wyrtki et al, 1981). Month of 1979 indicated for each data pair.

Figure 6. Deviation (δ_A) from annual longterm mean temperature at 160 m. Cold anomaly shaded, warm anomaly clear, insufficient data blank. Distribution of XBT stations received by radio at FNOC given by inset at lower left.

Figure 7. Winter mean sea level observed at islands compared to dynamic height 0/1000 db observed during the January cruise of *R/V Ryofu Maru* along 137°E, 1967 to 1977.


LEGEND
(10) NUMBER OF SECTIONS OBTAINED 1/79-6/80
8/79 START DATE IF NOT PRIOR TO 1/79
(6)
(18)
8/79
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(9)
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160°E
120°

FIGURE - 1

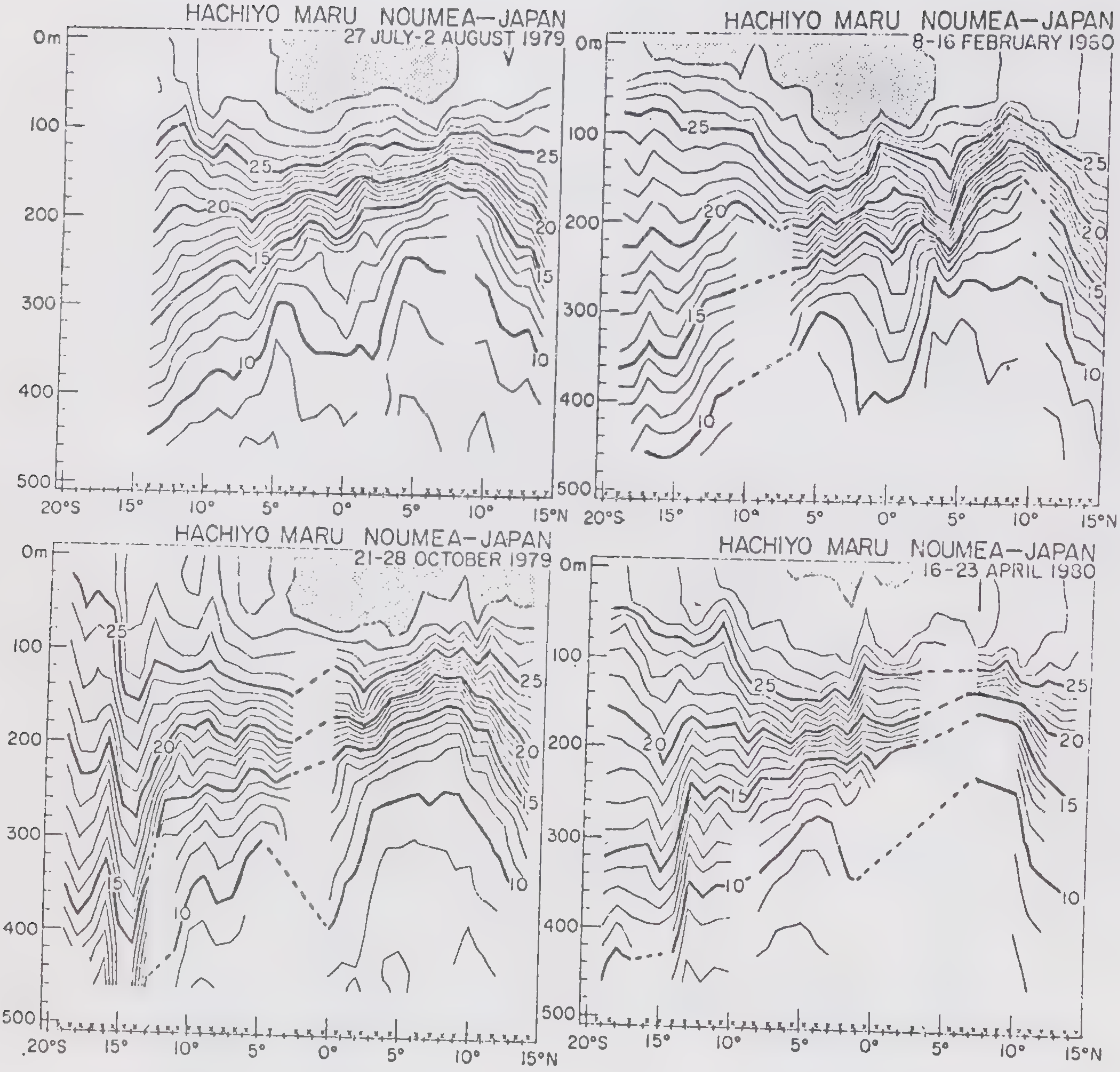
HACHIYO MARU NOUMEA—JAPAN
27 JULY-2 AUGUST 1979
HACHIYO MARU NOUMEA—JAPAN
8-16 FEBRUARY 1980
HACHIYO MARU NOUMEA—JAPAN
21-28 OCTOBER 1979
HACHIYO MARU NOUMEA—JAPAN
16-23 APRIL 1980
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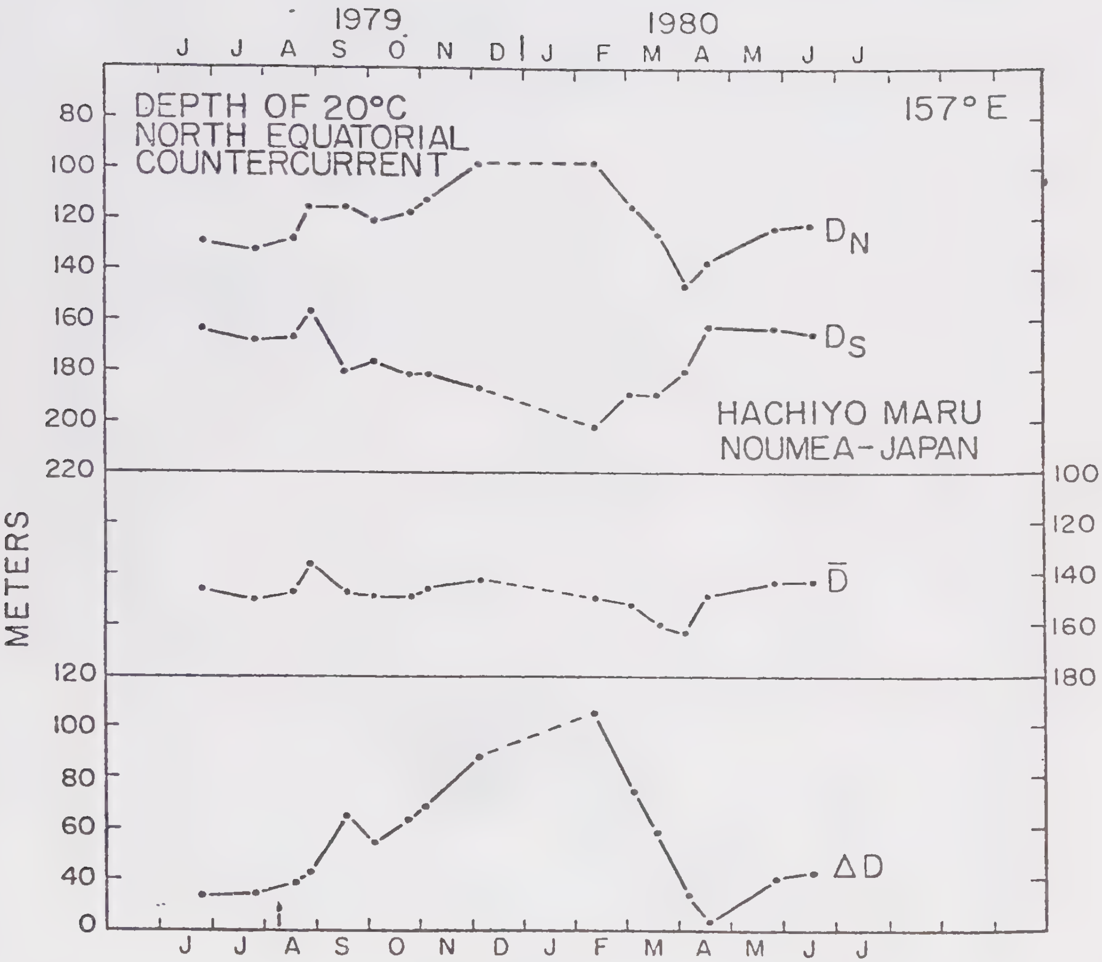
FIGURE - 2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1980
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DEPTH OF 20°C
NORTH EQUATORIAL
COUNTERCURRENT
157° E
80
100
120
140
160
180
200
220
D_N
D_S
HACHIYO MARU
NOUMEA-JAPAN
METERS
100
120
140
160
180
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120
100
80
60
40
0
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J J A S O N D J F M A M J J

FIGURE - 3

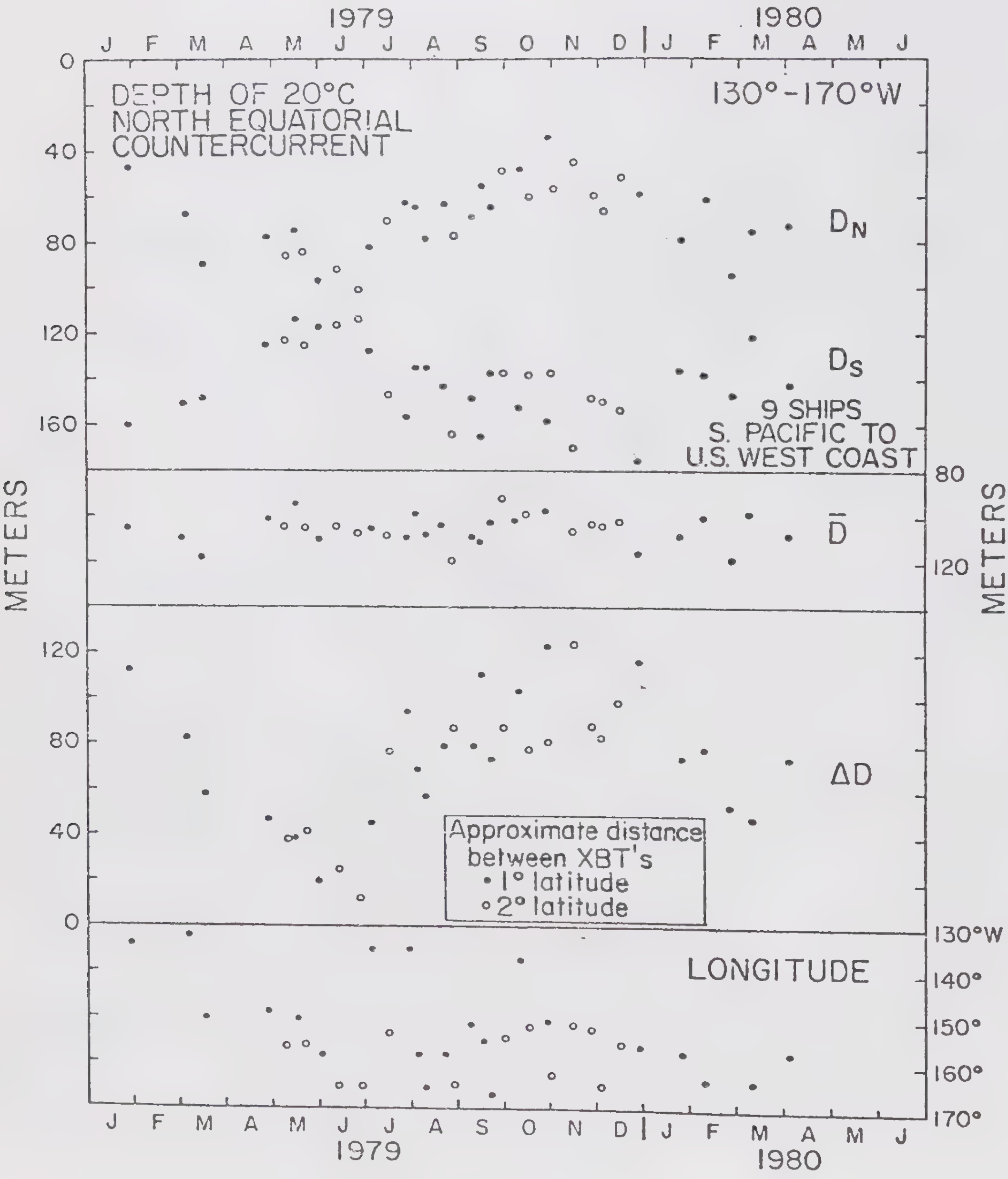

1979
1980
J F M A M J J A S O N D J F M A M J
DEPTH OF 20°C
NORTH EQUATORIAL
COUNTERCURRENT
130°-170°W
D_N
D_S
9 SHIPS
S. PACIFIC TO
U.S. WEST COAST
$\bar{D}$
ΔD
Approximate distance
between XBT's
• 1° latitude
∘ 2° latitude
LONGITUDE
METERS
0
40
80
120
160
80
120
0
40
80
120
130°W
140°
150°
160°
170°

FIGURE - 4

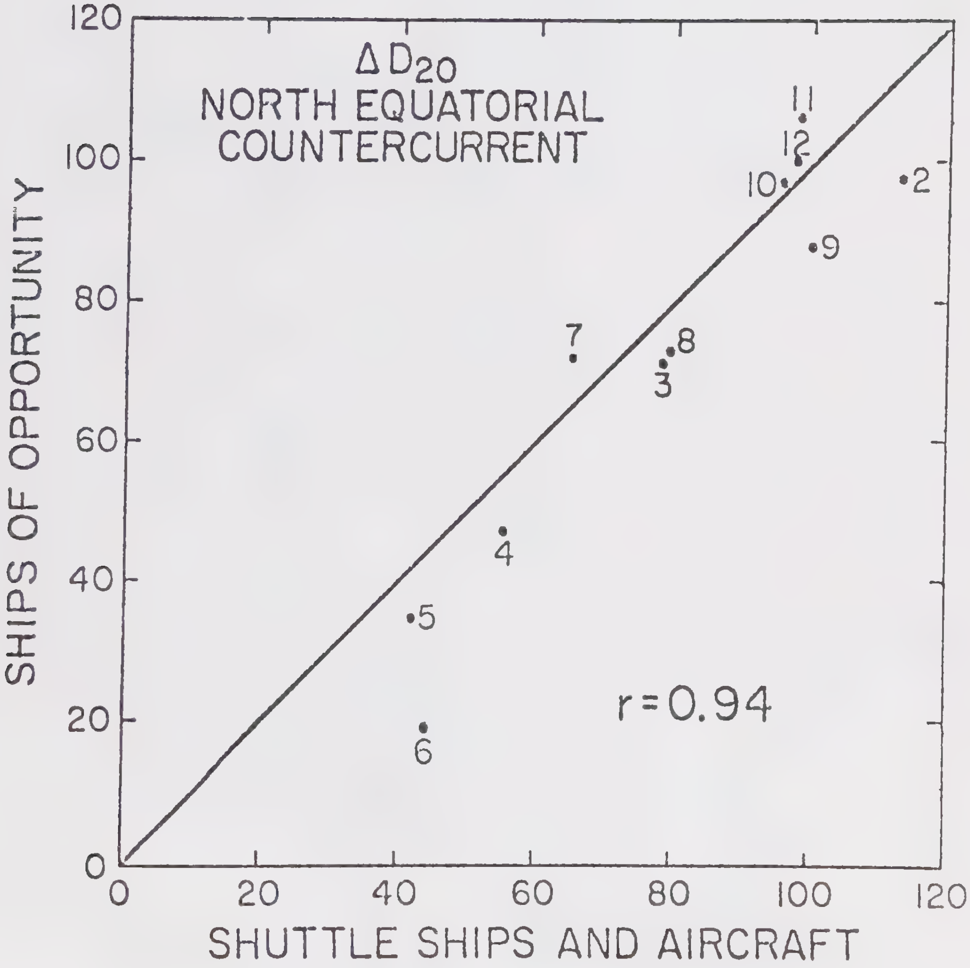

ΔD20
NORTH EQUATORIAL
COUNTERCURRENT
r=0.94
SHIPS OF OPPORTUNITY
SHUTTLE SHIPS AND AIRCRAFT
0
20
40
60
80
100
120
0
20
40
60
80
100
120
2
3
4
5
6
7
8
9
10
11
12

FIGURE - 5

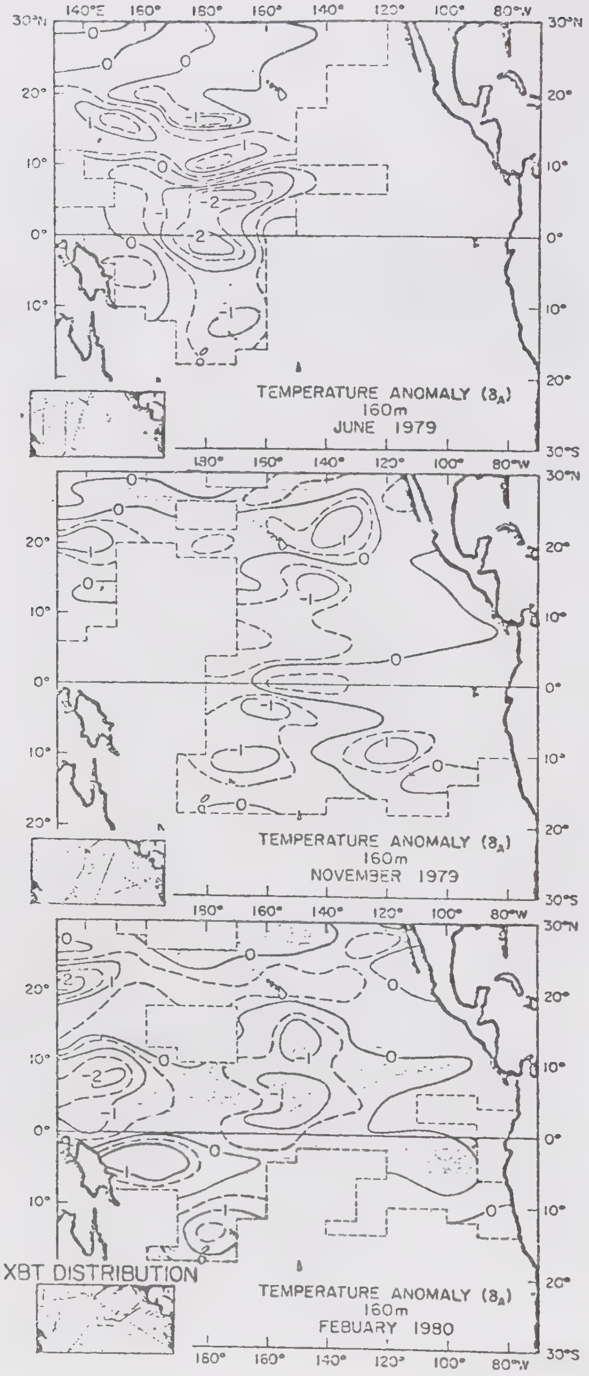
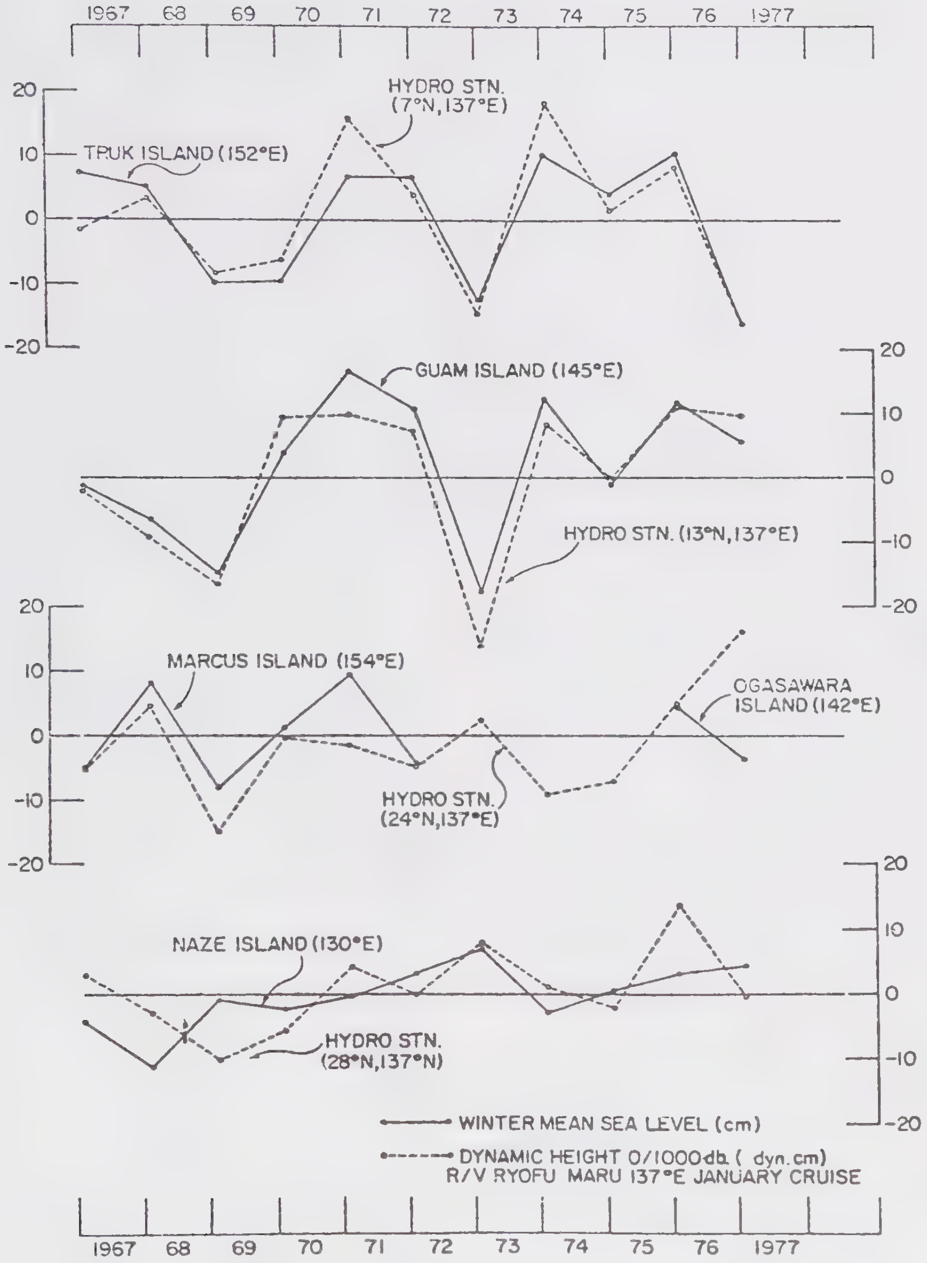

140°E
160°
180°
160°
140°
120°
100°
80°W
30°N
20°
10°
0°
10°
20°
30°S
TEMPERATURE ANOMALY (δA)
160m
JUNE 1979
TEMPERATURE ANOMALY (δA)
160m
NOVEMBER 1979
XBT DISTRIBUTION
TEMPERATURE ANOMALY (δA)
160m
FEBUARY 1980
0
-1
-2
1
2

FIGURE - 6



SEA LEVEL AND DYNAMIC HEIGHT
WESTERN TROPICAL PACIFIC

FIGURE - 7

8142

Rapp. P.-v. Réun. Cons. int. Explor. Mer, 178: 475-480. 1981.

SURVIVAL AND GROWTH OF NORTHERN ANCHOVY LARVAE ON LOW ZOOPLANKTON DENSITIES AS AFFECTED BY THE PRESENCE OF A *CHLORELLA* BLOOM

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First feeding northern anchovy, *Engraulis mordax*, were reared on low densities (100, 150 and 300 items/l) of wild zooplankton in a medium containing 10 000 to 19 000 cells/ml of the green alga *Chlorella*. After 16 days, mean survival was five times greater than, and growth equivalent to, that usually sustained in the laboratory at much higher food densities.

Feeding experiments, coupled with larval and dietary fluorescence measurements, showed that larvae not only ingest the small *Chlorella* cells, but are capable of substantial intestinal degradation of the algal cell wall and intracellular chlorophyll. Thus anchovy larvae potentially derive direct nutritional benefit from the algal cells. It was also shown that these larvae can derive indirect nutritional benefit from the algal cells present in the guts of well-fed zooplankton ingested by the larvae.

Therefore, it appears that northern anchovy larvae are capable of significant survival and growth at low zooplankton densities in the presence of dense algal blooms, because the larval diet is supplemented both directly and indirectly by algal nutrients.

INTRODUCTION

Most laboratory studies indicate that significant survival in larval fishes requires much higher food densities than those normally found in the sea (O'Connell and Raymond, 1970; Lasker et al., 1970; Theilacker and McMaster, 1971; Hunter, 1972, 1976, 1980; Hunter and Thomas, 1974). Several recent reports, however, suggest that a number of larval fishes are capable of significant survival and growth at low wild zooplankton densities (25, 50, 100, 150, 300 items/l) when reared in the presence of dense algal blooms (Detwyler and Houde, 1970; Houde and Palko, 1970; Saksena and Houde, 1972; Houde, 1972, 1973, 1974, 1975, 1977, 1978; Stepien, 1976; Houde and Schekter, 1978).

Houde and his colleagues believe that green water functions to reduce the detrimental effects of metabolic by-products which accumulate in a static rearing system. They further contend that *Chlorella* cells (<10 μm) are not purposefully ingested and, when taken accidentally, the larvae are not capable of breaking them down to derive nutritional benefit (Houde, 1973, 1975, 1977 unpublished research proposal). Green water may well function as these gentlemen suggest, however, it is unrealistic to assume that algal cells present in the gut do not provide at least minimal nutrient value for the larvae. Neither does their hypothesis consider the possibility that the green water actually provides a rich nutrient source for the zooplankton, thus enhancing the larval diet indirectly.

To investigate these possibilities, feeding and rearing experiments were performed on *Engraulis mordax* to determine the effects of low wild zooplankton densities with and without an algal bloom. Subsequently, fluorescence measurements of pure algal cultures and lab-cultured foods were compared with those of larvae fed various combinations of these cultures, to determine whether larvae potentially derive any direct or indirect nutritional benefit from the alga.

MATERIALS AND METHODS

In order to determine the feeding response of first feeding larvae to the presence or absence of the alga *Chlorella*, the dinoflagellate *Gymnodinium splendens*, and the rotifer *Brachionus plicatilis*, feeding experiments similar to these described by Lasker (1975) and Scura and Jerde (1977) were performed in blackened 8 liter battery jars submerged in a 17° C water bath. The light source (four, 40W daylight fluorescent bulbs) was suspended 60 cm above the surface of the feeding medium. Battery jars contained *Chlorella* blooms of densities varying from 0 to 19 000 cells/ml. To some of these jars *Gymnodinium* and *Brachionus* were added to achieve densities of 300/ml and 100/ml, respectively. To other jars no additional food was introduced. *Brachionus* were sieved so that only individuals <100 μm were offered as food for the lab-spawned, first feeding larvae. Algal and food density counts were made using a 16-channel model Ta Coulter counter. The larvae were allowed to feed for 3 h, after which the larvae were vacuum siphoned onto a nitex filter disc for microscopic inspection for feeding condition and gut fullness.

Rearing experiments were performed to evaluate the growth and survival of first feeding larvae at low zooplankton densities in the presence and absence of dense algal blooms. Rearing procedures were similar to those reported by Detwyler and Houde (1970); Houde and Palko (1970); Saksena and Houde (1972); Houde (1972, 1973, 1974, 1975) and Stepien (1976). Larvae were reared from first feeding (3 to 4 days after hatching) to 16 days in a static system consisting of 75 liter glass aquaria submerged in a 17° C water bath. Aquaria were filled with either sea water filtered to 1 μm or a dense *Chlorella* bloom (10 000 to 19 000 cells/ml) to within 2.5 cm of the rim. Low aeration was used to keep *Chlorella* cells in suspension. One-fifth of the rearing medium was exchanged bidaily, and fresh algal cells were added to maintain the culture. A light source similar to that described in the feeding experiments illuminated the aquaria on a 13 light, 11 dark light cycle. The initial stocking density was 2/l or 130/aquarium.

Wild zooplankton was collected three times weekly in 5 min surface to 1 m tows using a 3/4 m, 35 μm net. Zooplankters were segregated by size using nitex sieves and maintained at 10° C in glass aquaria containing high concentrations of *Chlorella* (5000 to 10 000 cells/ml). Approximately 95% of the zooplankters introduced to rearing tanks were various life stages of copepods.

On the fourth day after the larvae hatched, zooplankton between 35 and 64 μm (predominately copepod nauplii) were added to the tanks in densities of of 0/l, 100/l, 150/l or 300/l. Food levels were monitored daily (1200/ml/tank), and the appropriate zooplankton additions were made. Progressively larger food items (copepodites and small adults to 350 μm) were added during the 16-day experimental period. Larvae were sampled only at the termination of the experiment by siphoning the contents of each tank through a 150 μm sieve. Counts and total lengths of the survivors were determined and compared.

Larvae used for fluorescence measurements were allowed to feed for 3 h in the same manner described for the feeding experiments. Once vacuum siphoned onto a nitex filter, larvae were microscopically inspected, and 10–20 of those containing food items were placed on a ground glass filter. Known quantities of *Gymnodinium*, *Chlorella*, and both starved and *Chlorella*-fed *Brachionus* were also placed on separate ground glass filters.

Following procedures described by Holm-Hansen et al. (1965), each filter was ground in a tissue grinding tube with 5 ml of 90% acetone for 1 min, until the filter disintegrated. The resulting suspension was poured into a vial and the volume increased to 10 ml with acetone. Vials were stored in a refrigerator overnight to allow complete pigment extraction in the dark. The suspension was then centrifuged at 2 500 × g for 10 min and the supernatant decanted into a fluorometer tube and stored in the dark until fluorescence was measured.

To afford more consistent sensitivity the third slit of a Turner model 111 fluorometer was used exclusively. After the initial reading, three drops of 0.5 N HCl were added to the sample; within 1 min after thorough shaking, the second reading was taken. Acid factors for each sample were calculated by dividing the initial reading (the fluorescence of the chlorophyll *a* present before acidification) by the fluorescence of the chlorophyll *a* after acidification. Comparisons were made between the acid factors of lab cultures and those calculated for larvae and/or *Brachionus* containing ingested food items.

RESULTS

Results of feeding experiments indicate that of the larvae placed in a *Chlorella* bloom of at least 5000 cells/ml with no other food items present, about 20% had guts half- to completely-full of algal cells in 3 h. The degree of gut coloration was qualitatively proportional to the algal density in the feeding medium. Of those larvae offered either *Gymnodinium* or *Brachionus* in addition to the algal medium, over 50% contained accumulations of algal cells surrounding other ingested items. Larvae were not found to accumulate algal cells in the absence of light.

Forty to 60% of the larvae reared at 100 items/l in green water survived with a 67.5% increase in the mean total length (Table 1A and B). At 150 items/l survival varied from 31 to 84% with a mean length increase of 98%. Survival at 300 items/l in green water averaged 61.5% with a 72% length increase. When *Chlorella* cells were absent, survival rates were 6% or less at all

Table 1. Survival and growth percentages of *E. mordax* larvae reared for 16 days on wild zooplankton with and without a *Chlorella* bloom.

A. Larval Survival (%)

Chlorella present				*Chlorella* absent		
Zooplankton densities				Zooplankton densities		
0/1	100/1	150/1	300/1	100/1	150/1	300/1
0	45	31[a]	84[a]	0	1	0.8
0	44	63[a]	39[a]	6	4	
0	39[b]	39				
0	60[b]	44				
		64[b]				
		84[b]				
$\bar{x} = 0$	47	54	61.5	3	2.5	0.8

B. Larval Growth (% total length increase)

Chlorella present				*Chlorella* absent		
Zooplankton densities				Zooplankton densities		
0/1	100/1	150/1	300/1	100/1	150/1	300/1
0	35	58[a]	75[a]	—	12	78
0	70	65[a]	68[a]	12	40	
0	80	118				
0	85	82				
		120[b]				
		142[b]				
$x = 0$	67.5	97.5	71.5	12	26	78

[a] *Noctiluca* bloomed during the last 4 days of the experiment.

[b] Barnacle cyprid larvae contamination during last week.

three food densities with 28% mean total length increase.

The guts of surviving larvae commonly contained *Chlorella* cells in the "soup" surrounding ingested green copepodites and whole adult copepods. Zooplankters sampled daily from each aquarium ranged from clear in non-green water to very green in tanks containing *Chlorella*. During the last 4 days of the first experiment, *Noctiluca* "bloomed" in only the green tanks. These dinoflagellates were very green in color compared to the few sampled in non-green tanks. *Noctiluca* cells were observed in the guts of surviving larvae. During the last week of the third experiment, barnacle cyprid larvae (<40 μm) were a large contaminant of only the green tanks, although zooplankton additions were identical between tanks. These cyprids were not detected in the guts of surviving anchovies.

The Turner fluorometer had a fluorescence range from 1.0 for pure phaeophytin *a* (the breakdown product of chlorophyll *a*) to 2.0 for pure chlorophyll *a*. Table 2 gives the number of samples, the acid factor ranges and mean acid factors for the measurements made on pure cultures of *Chlorella*, *Brachionus* (starved and fed), and *Gymnodinium*, as well as the larvae fed these cultures.

Acid factor comparisons (Fig. 1) indicate that chlorophyll levels in *Gymnodinium*-fed larvae tended to be 25% lower than those measured for pure cultures of *Gymnodinium*. Comparison between pure *Chlorella* and *Chlorella*-fed larvae shows a 27% difference, presumably the result of the digestive activity of the larvae. Chlorophyll *a* levels decreased by 35% when *Chlorella* was ingested by *Brachionus*; larvae containing *Chlorella*-fed *Brachionus* show this same chlorophyll level. Similarly both starved *Brachionus* and larvae containing starved *Brachionus* show the same low level of chlorophyll. Starved larvae show the lowest chlorophyll level.

Table 2. Sample size, mean acid factors and ranges are given for fluorescence measurements made on each lab culture and the larvae used in each feeding treatment. Acid factors are an index of the phaeophytin a levels present (1.0 = pure phaeophytin and 2.0 = pure chlorophyll a). Phaeophytin is the metabolic breakdown product of chlorophyll.

Culture	Sample size	Acid ratio range	Mean acid ratio
Chlorella	8	1.56–1.78	1.66
Gymnodinium	6	1.83–2.00	1.93
Brachionus			
Starved	7	1.23–1.43	1.34
Chlorella-fed	6	1.37–1.58	1.43
Larval Feeding Treatments			
Starved	16[a]	1.00–1.30	1.12
Fed *Chlorella*	10[a]	1.15–1.64	1.48
Fed *Gymnodinium*	8[a]	1.53–1.89	1.70
Fed *Brachionus* (starved)	7[a]	1.10–1.57	1.35
Fed *Brachionus* (fed)	6[a]	1.33–1.62	1.45

[a] Each sample contained 10–20 larvae.

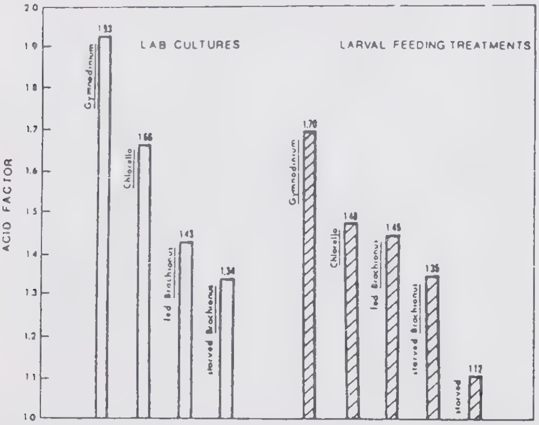

Figure 1. Bars represent the acid factors (relative chlorophyll *a* levels, where pure chlorophyll *a* = 2.0 and pure phaeophytin *a* = 1.0) for each lab culture or larval feeding treatment. Comparisons show that about 25% of the chlorophyll *a* in *Gymnodinium* and *Chlorella* is reduced to phaeophytin *a* by the larvae in 3 h. About 35% is reduced by *Brachionus*. Larvae fed *Brachionus*, either well-fed or starved, show no difference from these *Brachionus* cultures alone.

DISCUSSION

Laboratory and field evidence indicates that feeding in northern anchovy is highly size selective, limited primarily by mouth size and prey visibility (Hunter, 1972, 1980; Arthur, 1976). Lasker (1975) found that items smaller than 30 μm in effective diameter were taken rarely. In the present study, *E. mordax* first feeding larvae were found to accumulate *Chlorella* cells in the gut. This is somewhat surprising, since the effective diameter of *Chlorella* is <10 μm and first feeding larvae can not filter feed (Hunter, 1972). Since larvae were not found to accumulate algal cells in the dark, simple drinking of algal cells is unlikely. Therefore, it is feasible, particularly in light of the correlation between cell density in the medium and the degree of gut coloration, that while individual cells are not perceived, their cumulative presence and motion in the water stimulate some of the larvae to strike at the "green" mass. Thus algal cells are ingested in proportion to their relative abundance in the medium.

When offered either *Brachionus* or *Gymnodinium* in green water, larvae striking at the larger prey items ingest *Chlorella* cells whether prey capture is successful or not. This accounts for algal cell accumulations observed in rearing experiment survivors as well.

Zooplankton densities found previously to be required for 50% survival varies greatly between the northern anchovy, 4000 items/l (O'Connell and Raymond, 1970), and the species investigated by Houde (1975, 1977, 1978); 1751/l for bay anchovy, 199/l for sea bream, and 854/l for lined sole. Densities required for 10% survival were 900/l for northern anchovy (O'Connell and Raymond, 1970); and 75/l, 28/l and 115/l for bay anchovy, sea bream, and lined sole, respectively (Houde, 1975, 1977, 1978). Houde attributes the "significant" survival at lower food densities to lower stock densities, daily food monitoring and additions and the reduced metabolic by-product accumulations afforded by the algal bloom. By employing the same techniques described by Houde and his colleagues, northern anchovy survival averaged 47% at 100 food items/l, 54% at 150/l, and 61.5% at 300/l in green water. Survival in tanks where green water was absent was 6% or less.

Hunter (1977) calculated that about 230, 50 μm food items must be ingested and metabolized daily by a single first feeding anchovy in order to survive. Lasker (1975) showed that in order to fill or partially fill a larval gut in an 8 h feeding period, 20 to 40 items/ml are required in the feeding medium. The food levels available per larva in the present study (50, 75, 150/larva) were far below these "required" ones. Perhaps the differences can be partially explained by the presence of the dense *Chlorella* bloom, if the larvae are capable of breaking through the tough cell wall to digest and assimiliate any of the algal nutrients.

Holm-Hansen et al. (1965) show that the higher phaeophytin levels detected in phytoplankton field samples, as compared to pure lab cultures, are the direct result of grazing and the chlorophyll reduction processes of zooplankton. The acid factor of zooplankton fecal pellets is 1.05, indicating the total reduction of chlorophyll *a*. The evidence provided herein suggests that this is not only the case in grazing by *Brachionus*, but also in grazing by anchovy larvae. About 25% of the chlorophyll *a* in *Chlorella* and *Gymnodinium* is available to the larvae in only 3 h of their 5 h gut residence time. More would probably be detected at the end of 5 h and by the fluorescence of fecal pellets. The rather wide ranges observed in the acid factors may be correlated with the variability in larval gut fullness and differences in the onset of feeding between individual larvae. In the same length of time (3 h) 35% of the chlorophyll *a* in *Chlorella* is available to *Brachionus*. These results lend strong support to the direct availability of algal nutrients to anchovy larvae.

While *Chlorella* would never be encountered in nature by *Engraulis mordax*, since it is a fresh water alga, nor would the density of an alga be likely to reach such high levels, the evidence presented here emphasizes the fact that small particles can not be ignored as a potential source of nutrients either in the laboratory or under field conditions.

In these experiments, larvae fed *Brachionus* which had been fed *Chlorella*, show the same phaeophytin level as the culture of well-fed *Brachionus*. This suggests that the larvae need not process the *Chlorella* further upon ingesting and digesting *Chlorella*-fed *Brachionus*, and that they do actually benefit from the green water indirectly via the zooplankters. Theilacker and McMaster (1971) found that well-fed *Brachionus* provide a better food source for anchovy larvae than poorly-fed *Brachionus*.

I suggest that the presence of the dense algal bloom in the laboratory functions in the same manner described by Lasker (1975) and Smith and Lasker (1978) for the chlorophyll maximum layer under field conditions. Available primary producers are concentrated in a stratified layer, and thus, provide a rich feeding ground for grazing zooplankters, which in turn provide a concentrated food source for larger heterotrophs. The blooms of *Noctiluca*, high barnacle larvae survival, and the green zooplankters in the green rearing tanks simulated this effect in the laboratory.

While these conditions augmented survival in these experiments, growth rate was not significantly different from that sustained when anchovy were reared on a combination of *Gymnodinium* and *Brachionus* at much higher densities. Arthur (1977, 1980) suggests that larval feeding behaviour may be more active in the lab, enhancing heart and musculature development, while at the same time depressing growth by the greater metabolic demand of the activity. Hunter (1977) contends that prey items too small to quantitatively sustain growth exclusively, may indeed afford dietary supplement provided larger food items are also available. In addition, it may be that qualitatively, the nutrients available from the algal cells are not appropriate for growth, but serve to reduce the energy deficit between food items of the appropriate size and nutrient value and/or provide a more abundant supply of trace nutrients.

It is quite probable the presence of an algal bloom does stabilize water quality in a static rearing system, thus promoting the survival of fish larvae. Contrary to the reports of other investigators, this study indicates that the algal cells provide both direct and indirect supplement for northern anchovy larvae reared at exceptionally low food densities. Whether these contradictory results are due to subtle differences in rearing technique, interspecific differences or interpretation must be examined further. However, it is clear from this investigation that small organic particles, especially in large concentrations, can no longer be ignored as potential nutrient sources in future studies of larval fish ecology.

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Morphological and Functional Aspects of Marine Fish Larvae

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Morphological and Functional Aspects of Marine Fish Larvae

The notion that mortality during the larval stage is a major determinant of year class strength has been a part of fisheries theory since before the turn of the century (see Marr, 1956; May, 1974; Hunter, 1976, Lasker, this volume). I have been asked to talk about the systematic aspects of the larval stage, a subject as vast and diverse as systematic ichthyology itself. The importance of diversity to fisheries science is coming into prominence as we move beyond single species concepts. Since demersal and pelagic species from all depths supply larvae to the surface waters, nowhere else in the life histories of these species is there so great a potential for interaction. One might even characterize the larval stage as that period in ontogeny when major portions of a fish fauna come together and share prey, predators, and abiotic variables. Knowledge of direct and indirect species interactions during the larval stage will play an important role in the evolution of multispecies fisheries models.

The previous lecturers have discussed larval fishes from the points of view of behavior, physiology, and ecology. I would like to focus on the morphological aspects of larval adaptation. Marine teleost larvae have evolved an enormous array of morphological specializations, such that it seems we are looking at a distinct evolutionary domain quite separate from that of the adults. It is reasonable to assume that these remarkable structural specializations are adaptive and reflect each species' solution to the challenge of survival in a complex and demanding environment. In the course of an hour I could only hope to discuss a few of the adaptations found within selected teleost groups.

A good place to start is with a problem which puzzled Aristotle and remains somewhat of a puzzle today—the life history of the European eel, *Anguilla anguilla*. Since mature gonads were never found in the freshwater adults, their reproduction remained a mystery for millenia (Schmidt, 1932). Then just before the turn of this century, two Italian scientists, Grassi and Calandruccio (1897), captured some of the leaf-like marine larvae, known as leptocephali, and kept them in an aquarium, where they turned into the transparent glass eel stage of *Anguilla* (Fig. 1). Thus, it was shown that the species was catadromous. Seven years later Johannes Schmidt captured one of these leptocephali off the Faroe Islands north of Denmark. This initiated a wide-ranging plankton sampling program that employed four Danish research vessels and numerous merchant ships in the search for the newly

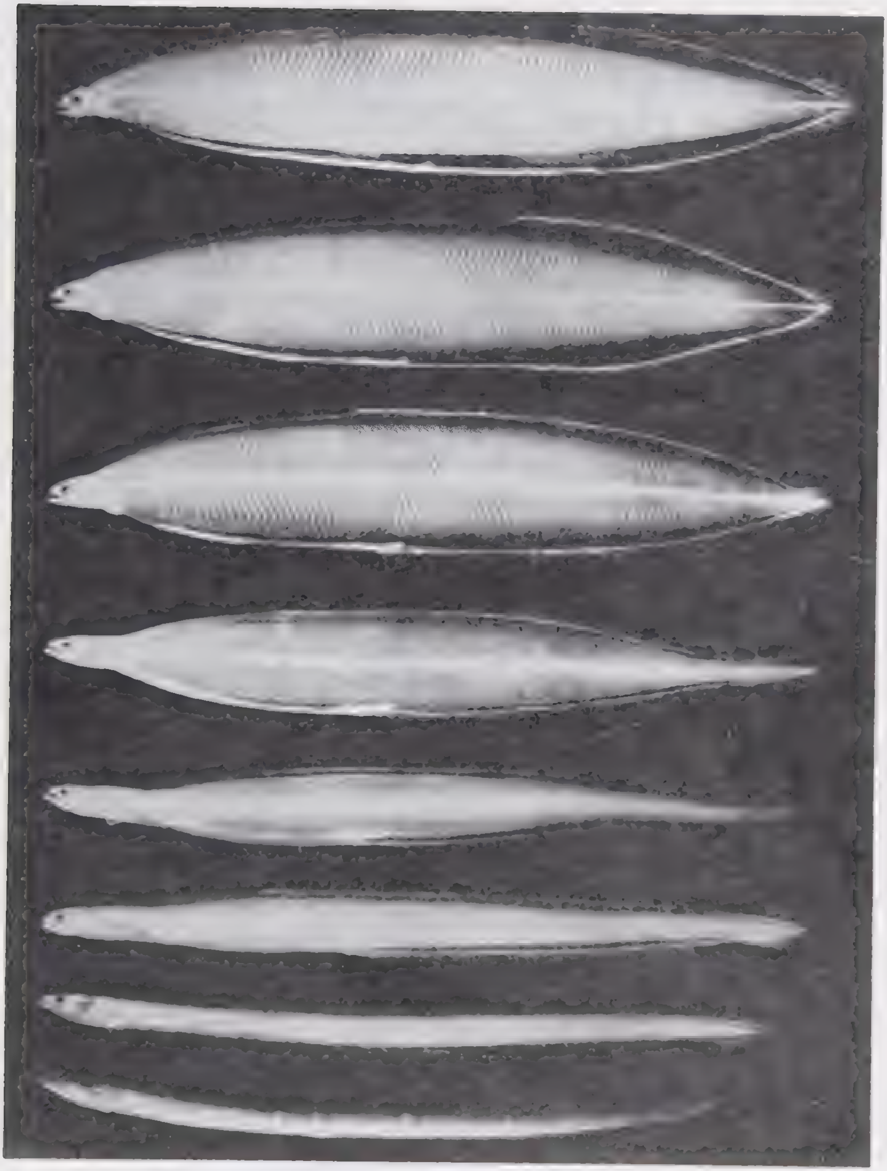

Figure 1. Transformation of the European eel, *Anguilla anguilla*, from the leptocephalus (at top, ca. 75 mm) to the juvenile (at bottom, ca. 64 mm). From Schmidt (1909).

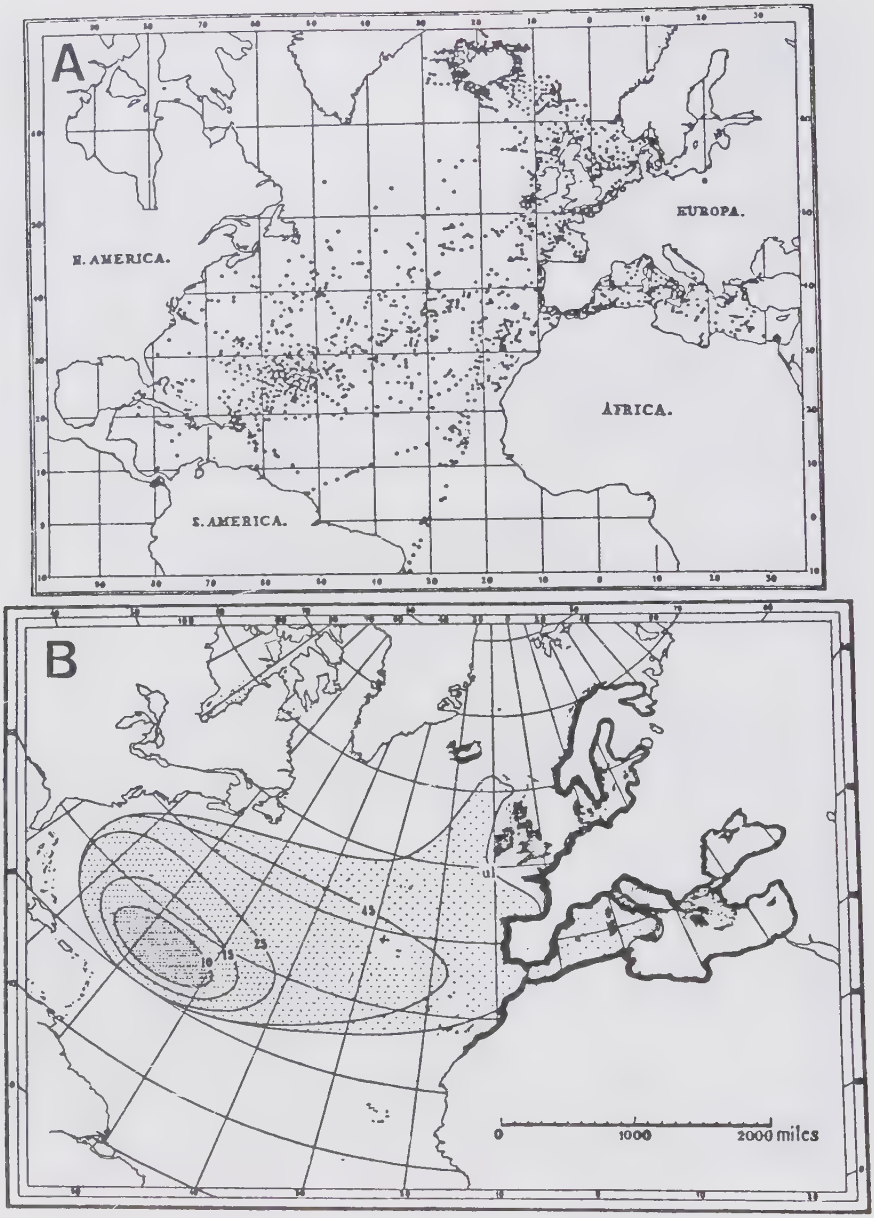

Figure 2. (A) Stations at which plankton collections were made during the Danish eel investigations, 1903-1922. (B) Areal distribution of *Anguilla anguilla* larvae based on plankton surveys. Contours indicate outer limits of occurrence of various sizes (mm) of larvae. Outermost contour refers to unmetamorphosed larvae. Black coastal strip shows distribution of juveniles and adults. From Schmidt (1925).

hatched larvae (Fig. 2). In 1922, with the discovery of newly hatched larvae in the Sargasso Sea, Schmidt concluded that ". . . the eels from Europe travel over the Atlantic to the Sargasso Sea where they spawn in the spring, and furthermore that the larvae, assisted by the North Atlantic current, make a journey in the opposite direction to Europe; a journey that lasts between two and three years" (Schmidt, 1932). Schmidt's research program was the progenitor of the type of wide-ranging ichthyoplankton survey that continues to be a valuable tool in answering fundamental questions about the life histories of marine teleosts.

Since anguillid eels are a tropical group, the migration of *A. anguilla* adults from the fresh waters of Europe to the Sargasso Sea and the slow return journey of their larvae (via the clockwise North Atlantic gyre) may have been the mechanism by which this species penetrated northward to the fresh waters of Europe. The possibility that the intercontinental journeys of this species have evolved gradually in relation to continental drift and the widening of the Atlantic during the Cretaceous, as suggested by Hulet (1978), in no way diminishes the immensity of the adaptations involved.

The nutrition of the eel larva during its journey is enigmatic since no food has ever been found in the gut of any eel leptocephalus. Furthermore, the gut is poorly differentiated and the lumen of the midgut is often occluded. The suggestion that dissolved organic compounds are absorbed directly through the epidermis is plausible since the epidermis is only from one to several cells thick and the surface cells are covered with microvilli (Hulet, 1978). Such a mode of nutrition would be remarkable since the leptocephali of some eels are the largest of all fish larvae. The leptocephalus of *Thalassenchelys coheni* attains a length of 30 cm (Smith, 1979) and a 25-cm specimen of this species in our care has a wet weight of 21 gm. The highly attenuate leptocephalus of a notacanthiform eel known as *Leptocephalus giganteus* attains a length of 184 cm (Nielsen and Larsen, 1970).

Hulet (1978) has suggested that an alternative nutritional source might be afforded by the extraordinarily large fang-like teeth typical of eel leptocephali. They could be used to puncture organisms and the protoplasmic juices could be swallowed and absorbed by the epitheleum of the esophagus and stomach. Such predaceous strategy might account for the emphasis on eye development and for the many eye specializations found among the eel leptocephali (Smith, 1979). If dissolved organic compounds are the source of leptocephalus nutrition, then the function of the huge teeth becomes problematical. Often it has been suggested that they could function in calcium metabolism. Considering the duration of the larval stage for many eels, another possibility is that they could serve as a defense against predators.

In addition to the 22 families of anguilliform eels and the three families of notacanthiform eels, leptocephali are found in the Order Elopiformes, a group which includes the tarpons, bonefishes, and ladyfishes. This was a major character used by Greenwood et al. (1966) to group the three orders into the Supraorder Elopomorpha.

Elopiform leptocephali share many morphological features with eel larvae, including the leaf-like body form, fang-like teeth, well-developed eyes, and distinct renal blood vessels, but differ markedly in having a well-developed caudal fin that is separate from the dorsal and anal fins. The caudal fin ray formula of elopiforms (10 + 9 principal rays, 4 + 3 hypurals, multiple ural centra) is also typically found in the next orders we will consider—the Clupeiformes, Salmoniformes and Myctophiformes (Ahlstrom and Moser, 1976).

Clupeiform larvae have elongate bodies with long straight intestines and are characterized by their relative uniformity and subtlety of morphological specialization (Fig. 3). Likewise, their conservative pigment patterns are dominated by serially arranged melanophores along the gut and on the ventral midline between the anus and caudal fin. It seems probable that, when expanded, the gut melanophores help conceal the larvae by masking light refracted from gut contents. Similarly, the melanistic shield which forms over the gas bladder reduces light refraction as a visual cue to potential predators. The melanistic pigment found on the oil globules of so many teleost eggs and yolk sac larvae may function in a similar way. Linear gut pigmentation and dorsal gas bladder pigment are recurrent larval characters represented in almost every teleost group in a myriad of arrangements, their universality attesting to their adaptive contribution.

Suggesting a function for the linear series of post-anal melanophores poses more of a problem. Since larvae are transparent and have a body outline that is imperceptible, or nearly so, it is unlikely that the post-anal linear series functions in concealment in the sense that Cott (1940) has shown for organisms with distinct body outlines. Moreover, if post-anal series were to function in this manner one would expect the pigment to be in the form of bars or saddles running at right angles to the body edge. Indeed, in a host of teleost species, melanistic bars and saddles are found in late larvae and pelagic juveniles, ontogenetic states where body outline is more likely to be an important cue to predators. Rather, it would seem that the distinctive post-anal melanophore series, present in so many species throughout almost every teleost group, would call the attention of potential predators. This does not negate the possibility of a protective role for post-anal pigment, since the zoological realm provides numerous examples where visual prominence of a prey species affords protection from predators.

One such example, the phenomenon of "flicker fusion," might be responsible for the widespread occurrence of post-anal melanophore series in teleost larvae as suggested by Joseph Copp (pers. comm.) of Scripps Institution of Oceanography. Describing the phenomenon in banded snakes, Shaw and Campbell (1974) state the following:

> As the snake moves forward, seeking a hiding place, the bands on its back follow one another like the spokes on a wheel. Depending on the nearness of the predator, the width of the bands and the intensity of the light on the snake . . . the results may be startling. At the very least an astigmatic

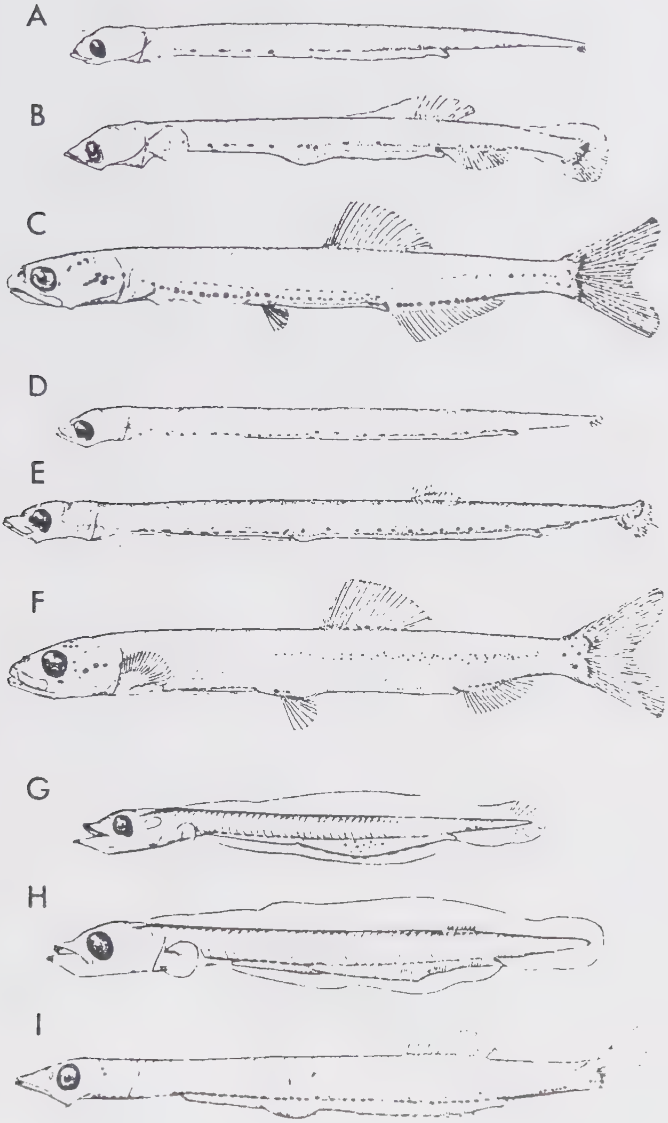

Figure 3. Larvae of clupeiforms. (A-C) northern anchovy, *Engraulis mordax*, 7.5, 11.5, 31.0 mm, from Kramer and Ahlstrom (1968); (D-F) Pacific sardine, *Sardinops sagax*, 9.1, 14.0, 31.3 mm, from Kramer (1970); (G-I) round herring, *Etrumeus teres*, 5.6, 8.2, 16.7 mm.

> condition may be produced in the onlooker. Most often, however, the flicker fusion phenomenon brings a fusing in the beholder's perception of the snake's bands, a greying of them, to the point where bands and the snake no longer exist. The beholder stares fixedly at the spot where he first saw the snake and misses the fact that the snake is passing from his view.

The serially arranged post-anal melanophores of teleost larvae may function in just this manner, and indeed the obfuscation may even be more effective owing to the rapid lateral beats of the larval tail. Flicker fusion may be another reason for the widespread occurrence of serially arranged lateral gut melanophores, and the effect may be even further heightened in species where the lateral gut series and the post-anal series form a continuum. Another possible adaptive advantage of melanophores is related to the specificity of their pattern. Melanophore pattern is one of the most useful characters for distinguishing among species of teleost larvae. It is possible that unique melanophore patterns could serve an infraspecific recognition function and aid in the location and exploitation of food patches. That is, the feeding movements of one or more larvae of a species, made visible and instinctively recognizable by their unique melanistic pattern, could serve to attract other members of the species to the patch and thus provide a selective advantage. This hypothesis is consistent with the survival premium placed on patch feeding as a compensation for overall low prey densities (outlined in Dr. Hunter's lectures), and one could see how such a mechanism could lead to the proliferation of the intricate melanophore patterns, so characteristic of teleost larvae. Additionally, in many schooling fishes (e.g., clupeiforms) the onset of schooling is within the larval phase, and here again melanophore pattern may be an important factor in intraspecific recognition. One could even speculate that the behavioral mechanisms of early larval patch feeding could have been intimately involved in the evolutionary origin of schooling and other aggregation phenomena.

A remarkable feature of clupeiform larvae, which they share with elopiforms, is the phenomenon of fin migration. Fage (1920) and Lebour (1921) described how, in the late larvae of many clupeiforms, the dorsal and anal fins migrate anteriad with respect to the myomeres. Anterior migration of the dorsal fin is greatest in the European pilchard, where the fin moves forward 11 myomeres during transformation. In the herring and sprat the fin migrates 7 and 5 myomeres respectively. Anterior migration of the anal fin is less pronounced in the above species (1, 6, and 4 respectively). In the Pacific sardine the dorsal fin migrates 10 myomeres and the anal fin 6, whereas in the northern anchovy the migration is barely perceptible (dorsal, 3; anal, 1). The functional significance of fin migration is unknown; perhaps the more posterior placement of the dorsal and anal fins during the larval stage could involve them in tail beat thrust.

In salmoniform fishes the larvae have undergone an extraordinary radiation, particularly among two deep-sea groups—the argentinoid smelts and the stomiatoids. These fishes have invaded deep oceanic waters, and the morphological specializations of the larvae must have played an important role

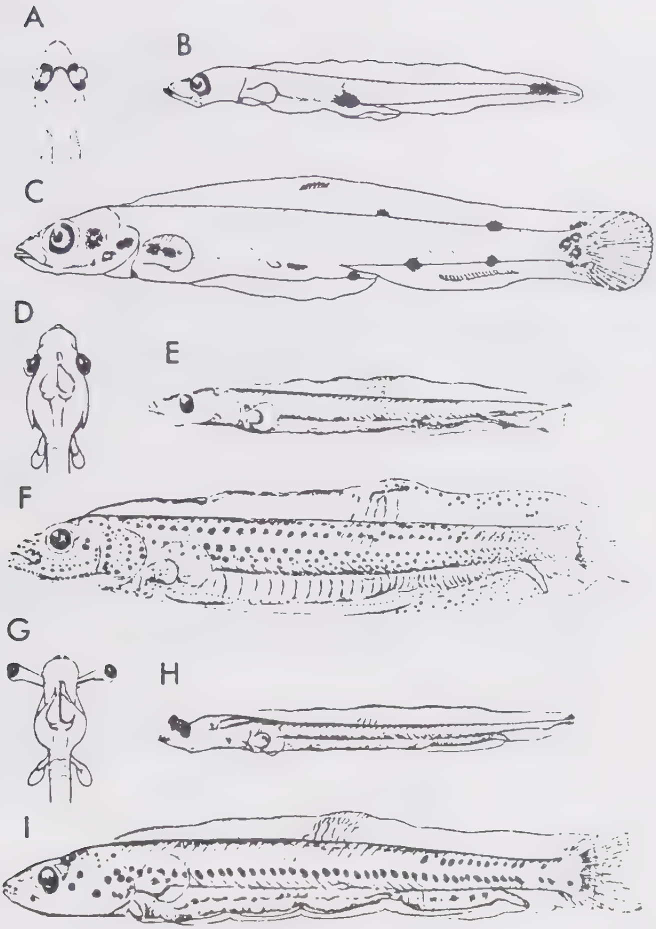

Figure 4. Larvae of argentinoid smelts showing various eye types. A-C, *Bathylagus milleri* with round eyes: (A) dorsal view of head of 10.6-mm larva, (B) 10.6-mm larva, (C) 27.5-mm larva; (D-F), *Bathylagus wesethi* with elliptical eyes, (D) dorsal view of head of 8.5-mm larva, (E) 8.8-mm larva, (F) 24.5-mm larva, from Ahlstrom (1965); G-I, *Bathylagus ochotensis* with stalked elliptical eyes, (G) dorsal view of head of 8.5-mm larva, (H) 10.2-mm larva, (I) 21.5-mm larva.

in the penetration and exploitation of this demanding environment. The fin fold has become a prominent feature and, in many salmoniforms, the dorsal and anal fins develop within the fin fold tissue at some distance from the body. The extreme is found in some argentinoids where the dorsal and anal fins form at the fin fold margin and are connected to the body by a series of hyaline strands (Fig. 4). At metamorphosis the fins become connected with the body in the normal position. The voluminous fin folds may enhance buoyancy and are probably involved in locomotion by high frequency/low amplitude vibration as Hunter (1972) has described for anchovy larvae in the S-strike position. The peripheral location of the developing dorsal and anal fins in argentinoids may serve to support the fin fold while allowing maximum freedom for vibratory locomotion.

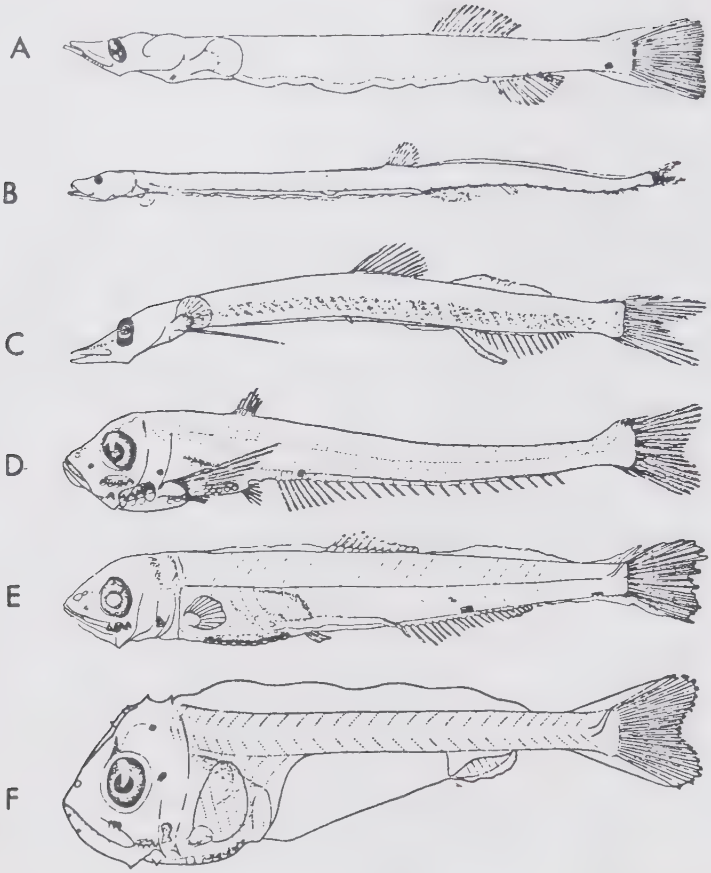

Figure 5. Larvae of stomiatoids. (A) *Vinciguerria lucetia*, 9.0 mm, from Ahlstrom and Counts (1958); (B) *Diplophos taenia*, 44 mm, from Jespersen and Taning (1919); (C) *Ichthyococcus ovatus*, 15 mm, from Jespersen and Taning (1926); (D) *Danaphos oculatus*, 22.4 mm, from Ahlstrom (1974); (E) *Maurolicus muelleri*, 10.3 mm, from Okiyama (1971); (F) *Sternoptyx* sp., 8.8 mm.

A characteristic of argentinoid larvae is the specialization of the eye. In many species the eyes have become narrowed and elliptical and in some species they are borne on stalks (Fig. 4), the possible function of which we can consider when we take up the stomiatoids.

The Stomiatoidei is dominated by two major groups, the gonostomatids and relatives and the melanostomiatids and their relatives. Gonostomatid larvae have achieved a diversity of form (Fig. 5). Some, such as the clupeoid-like *Vinciguerria*, are slender with a long intestine. *Diplophos* and *Ichthyococcus* are even more attenuate, and in the latter the posterior section of the elongate intestine trails free from the body (a feature that is widespread throughout the melanostomiatids) and the lower pectoral fin rays are extraordinarily elongate (a condition encountered in the larvae of some myctophid

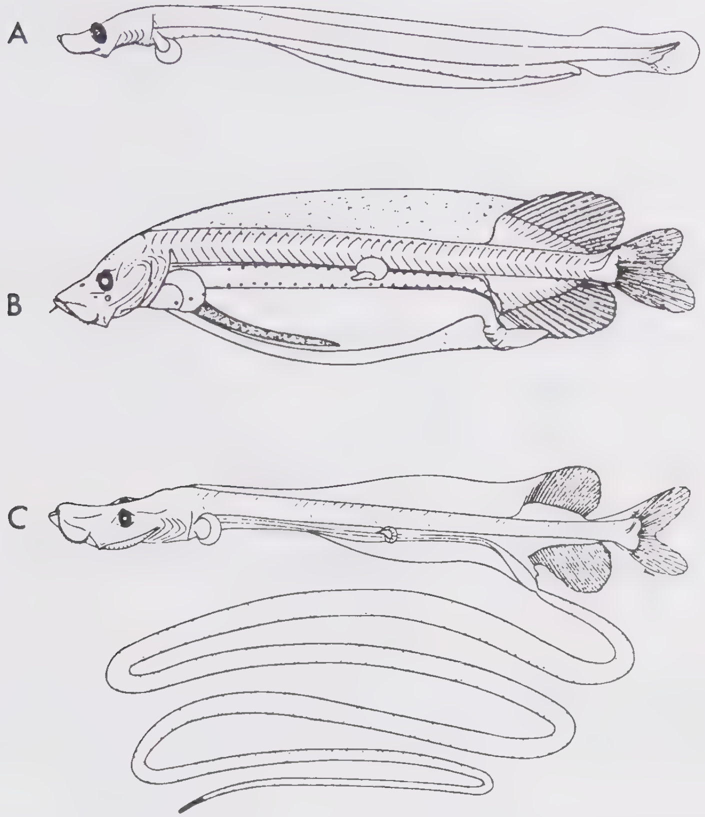

Figure 6. Larvae of stomiatoids. (A) *Stomias atriventer*, 10.0 mm; (B) *Bathophilus nigerrimus*, 21.7 mm, from Sanzo (1931); (C) Melanostomiatid, 34.5 mm.

species). In another direction, genera such as *Maurolicus* and *Danaphos* are less attenuate, have shorter intestines, and begin to develop their clumps of photophores well before transformation. The foreshortening of the gut, deepening of the body, and development of larval photophore clumps is most pronounced in the larvae of hatchet fishes, a group closely allied with the gonostomatids.

Morphological specialization reaches a zenith in larvae of the Melanostomiatidae and relatives (Fig. 6). They range from highly attenuate forms with long intestines such such as *Stomias* to rather deep-bodied forms such as *Bathopyhilus* with its voluminous sac-like intestine. The large jaws and expansive gut of the latter would appear to allow it to utilize large prey. Elongation of the gut beyond the confines of the body is a common feature of many melanostomiatid genera, and nowhere is this more apparent than in a larva tentatively identified to the genus *Leptostomias* (Fig. 6), where the gut is five times the length of the body and exceeds it in mass. One may speculate that, in this remarkable expression of alimentary dominance, digestion and absorption efficiency is improved while permitting a greater variety of prey types.

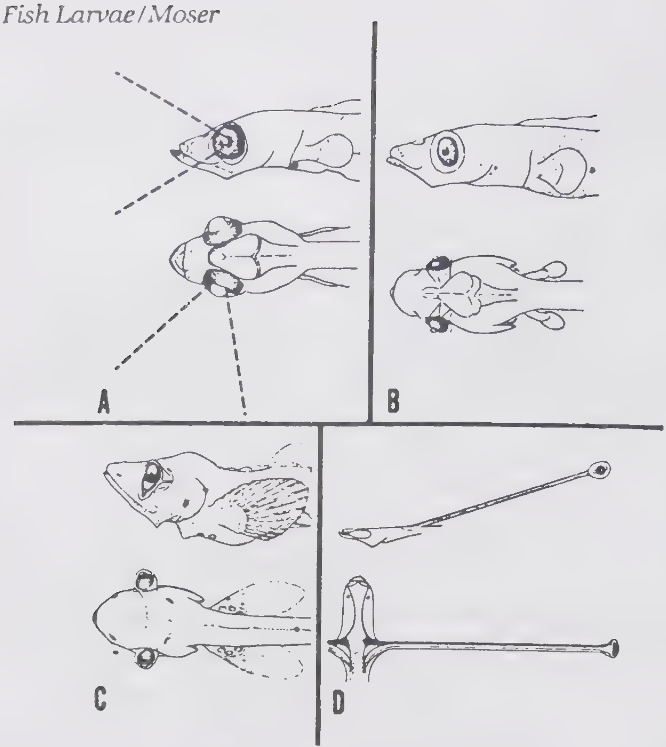

Figure 7. Various eye shapes of marine teleost larvae. (A) Round eye of *Bathylagus milleri*, lateral view (above) of 10.6-mm larva and dorsal view (below) of 9.5-mm larva; (B) Narrow sessile eye of *Bathylagus wesethi*, lateral view of 8.8-mm larva and dorsal view of 8.5-mm larva; (C) Narrow slightly stalked eye of 7.0-mm *Myctophum nitidulum* larva; (D) Markedly stalked eyes of 16-mm *Idiacanthus fasciola* larva. Figure from Weihs and Moser (1981).

Among the most specialized of all fish larvae are those of the stomiatoid family Idiacanthidae (Figs. 7 and 8). The eyes are borne on stalks that grow to one-fourth the length of the body and are then resorbed at transformation. Weihs and Moser (1981) have proposed a theory that might explain the adaptive advantage of this extraordinary specialization. If one assumes that the major causes of larval fish mortality are starvation, predation, and the interactions between them (Hunter, 1976), and that feeding and predator avoidance are largely dependent on vision, then eye specializations that improve feeding efficiency and predator avoidance are to be expected. Hunter (1972) showed that anchovy larvae notice and strike at food particles located within a 60° cone with a maximum height of about one body length and demonstrated that sighting distance and visual field are major limitations for feeding larvae.

Weihs and Moser (1981) suggest that enlargement of the visual field has evolved progressively through several stages, the first being a narrowing of a sessile round eye (Fig. 7B). In contrast to the round cup-shaped eye which lies flat in the developing orbit, the elliptical eye would have an increased rotational ability around the long axis, thus enlarging the volume observable from a given point. The next stage would be the extension of the eyes on short

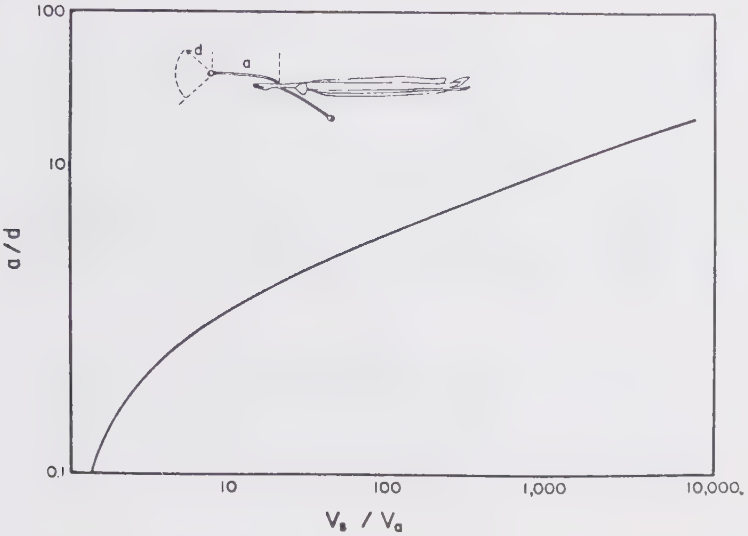

Figure 8. Theoretical relation of eye stalk length to perception distance in fish larvae. Ratio of the volume sighted by stalked eyes Vs to that covered by fully rotatable eyes attached to the head Va, versus the ratio of stalk length "a" to perception distance "d." *Idiacanthus* larva is shown to illustrate the geometrical parameters. From Weihs and Moser (1981).

stalks so that they lie just outside the margin of the eye (Fig. 7C). Such eyes could be even more freely rotated so that the observable volume would approach that of a sphere. Extension of the eyes on pedunculate stalks would further increase this volume (Fig. 7D).

These specializations raise the possibility of detecting prey from greater distances with a minimum of body motion, thus both conserving energy and reducing predator cues. Weihs and Moser (1981) calculate a tenfold increase in visual volume for elliptical eyes compared with round eyes and as much as an additional tenfold advantage for eyes borne on stalks (Fig. 8). The fact that protruding eyes have evolved independently in larvae of three families of anguilliform eels, in argentinoid and stomiatoid salmoniforms, and in the myctophiform lanternfishes points to the evolutionary value and persistence of the adaptation.

The order Myctophiformes is in some ways the most varied and interesting teleost order from the standpoint of larval development. Shallow-water benthic forms such as the synodontid lizardfishes have elongate larvae with long strait intestines, reminiscent of clupioid larvae (Fig. 9A). The large conspicuous melanistic blotches spaced evenly along the sides of the gut are characteristic of lizardfish larvae. Other benthic forms such as *Aulopus* and *Chloropthalmus* have shorter intestines with a single dorsally located melanistic blotch (Figs. 9B,C). Some deep-living benthic and benthopelagic forms have larvae with magnificent enlarged diaphanous fins (Fig. 9D). Larvae of the pelagic myctophiforms display great diversity of form. Notosudids have

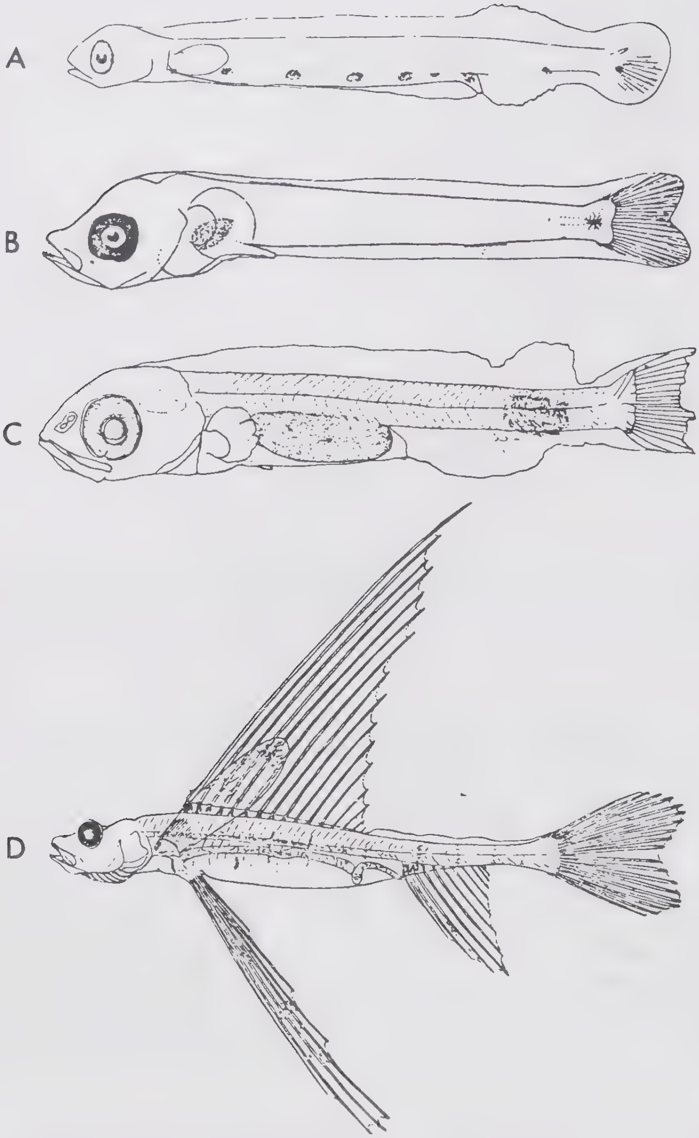

Figure 9. Larvae of demersal myctophiforms. (A) *Synodus lucioceps*, 10.5 mm; (B) *Chloropthalmus agassizi*, 9.5 mm, from Taning (1918); (C) Aulopid, 12.3 mm, from Okiyama (1974, courtesy of Springer-Verlag New York, Inc.); (D) Bathysaurid, 33 mm, from Marshall (1961).

elongate larvae with narrow elliptical eyes and curiously complex melanophore patterns in the caudal region (Fig. 10A). Larvae of the paralepidids, midwater predators, are elongate and have extremely short intestines that lengthen markedly during the larval stage. Their characteristic pigmentation consists of large melanistic blotches that are added serially along the dorsal aspect of the gut as it elongates and may function in maintaining a masking capability commensurate with gut length (Fig. 10C-E). Larvae of another

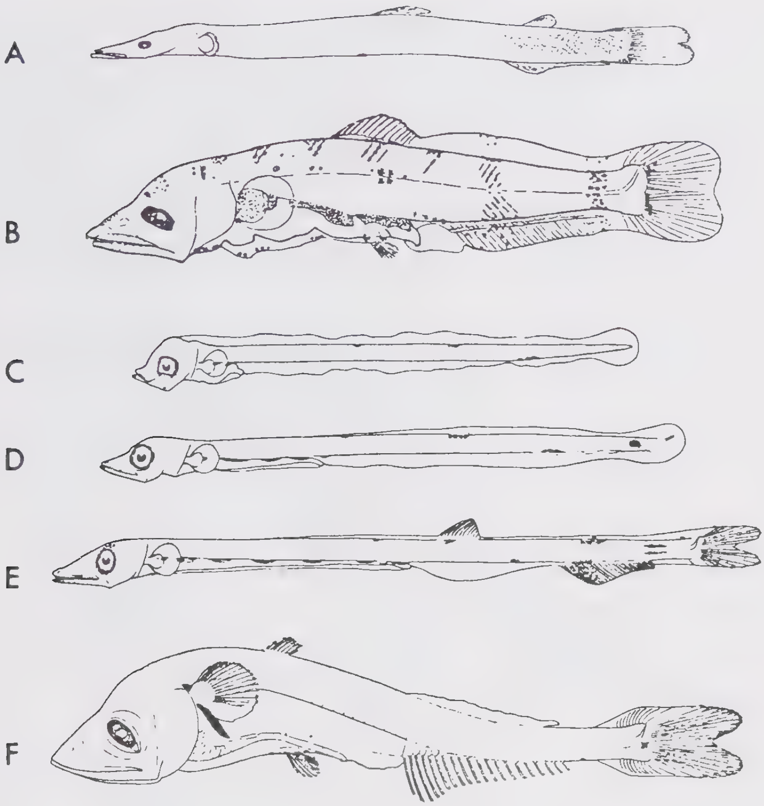

Figure 10. Larvae of midwater myctophiforms. (A) *Ahliesaurus berryi*, 30.5 mm, from Bertelsen et al. (1976); (B) *Evermannella balbo*, 11.5 mm, from Schmidt (1918); (C-E) *Lestidiops ringens*, 9.4, 16.5, 28.5 mm; (F) *Scopelarchoides nicholsi*, 23.0 mm.

midwater predatory group, the Scopelarchidae, have large jaws and a short bulbous gut that is covered by one or two very large melanistic blotches positioned directly over the saccular portion of the gut (Fig. 10F). Larvae of this group have also developed remarkably narrow eyes with pendant chorioid tissue.

In no other teleost group have the larvae explored so many pathways of evolutionary diversity as in the myctophid lanternfishes. As the largest family in the order (more than 30 genera and about 200 species), myctophids are ubiquitous in the world ocean. In a typical oceanic plankton tow about half the total fish larvae are those of lanternfishes, and Barham (1970) may be justified in suggesting that lanternfish have the largest biomass of any vertebrate group. Dr. E.H. Ahlstrom and I have been studying lanternfish larvae from a taxonomic viewpoint for over fifteen years, and our findings are detailed in four papers (Moser and Ahlstrom, 1970, 1972, 1974; Ahlstrom et al., 1976). Today I will only have time to describe some of the most prominent morphological specializations and discuss possible adaptive significance.

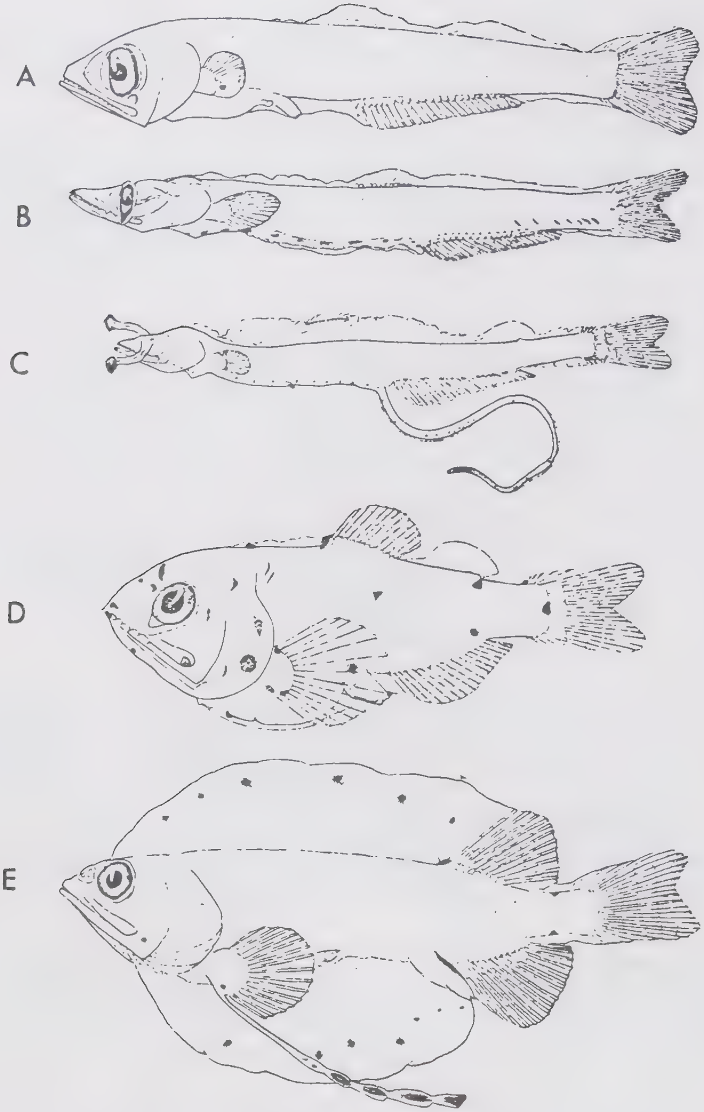

Figure 11. Larvae of myctophine lanternfishes. (A) *Protomyctophum crockeri*, 14.2 mm, from Moser and Ahlstrom (1970); (B) *Hygophum reinhardti*, 12.8 mm, ibid; (C) *Myctophum aurolaternatum*, 26.0 mm, from Moser and Ahlstrom (1974); (D) *Myctophum asperum*, 6.8 mm, ibid; (E) *Loweina rara*, 17.6 mm, from Moser and Ahlstrom (1970).

Paxton (1972) divided the family into two subfamilies, Myctophinae and Lampanyctinae, on the basis of adult osteology and photophore characters. Moser and Ahlstrom (1970) showed that characters of the larvae also divide the family, with a distribution of genera that mirrors that of Paxton. Myctophine larvae have narrow elliptical eyes and most lampanyctine larvae have round eyes, although some genera (*Triphoturus*, *Notolychnus*, *Lobianchia*) of the latter have experimented with narrowing of the eye (Figs. 11–14). Stalked eyes are found in three of the narrow-eyed myctophid genera. Practically every larval teleost body form is represented among myctophid genera, and we have been able to delineate a unique larval morph for each genus. Body form ranges from slender to stubby to leaf-like. The uncoiled intestine has distinctive transverse rugae and ranges from short, to elongate, to trailing free from the body (Fig. 11). The intestinal rugae, which are pronounced enough in myctophids and relatives to serve as an identifying character of the group, provide a mechanism for increasing the digestive and absorptive surface of an uncoiled gut.

Myctophid larvae exhibit a diversity and specificity of melanophore pattern that is unmatched among teleosts, and indeed each genus has a pigment morph that is as taxonomically useful as the structural morph. I believe that the specificity and often limited variation of pigment patterns in this group, perhaps in concert with the unique structural morphs, relate to the species recognition/patchfeeding idea presented earlier in the lecture.

A remarkable feature of lanternfish larvae is the development of one or more pairs of photophores, a character we saw in gonostomatids and sternoptychids. Larvae of almost every lanternfish species develop a photophore (later to become the middle branchiostegal photophore of juveniles and adults) below each eye. Considering the position and universality of occurrence of these photophores it is reasonable to suggest that they are functional and may lure and/or illuminate potential prey.

Additional pairs of photophores develop during the larval stage in three myctophine genera (*Benthosema, Diogenichthys, and Myctophum*) and in numerous lampanyctine genera. These additional photophore pairs appear consistently in several areas—anterior to the eye, on the outer surface of the pectoral fin pendunce, and along the ventrum. The preorbital photophores, like the branchiostegal photophores, may be utilized in feeding. The light organs on the highly motile pectoral fin base may also be involved in feeding, possibly as lures. Typical locations for the ventral organs among the various genera are below the pectoral fin base, just anterior to the developing pelvic fin, and posterior to the anus; however, the sequence of appearance of the photophores is often highly specific (Figs. 12–14). In genera such as *Diogenichthys* (Fig. 12), where the sequence of appearance of multiple photophores is highly specific, the photophore patterns may function as infraspecific recognition signals in feeding as suggested for the melanophore patterns. Since each photophore has a heavily melanistic cup, they could enhance the specificity of the melanophore patterns during the day and provide a specific luminous pattern during dim light conditions.

In larvae of two genera (*Loweina* and *Tarletonbeania*) the lowermost pectoral finrays become elongate and bear serially arranged pigmented fleshy spatulations (Fig. 11E). These elongate ornamented rays, along with some neighboring rays, are resorbed at transformation. Larvae of these same genera have voluminous fin folds which are accommodated by the posteriad

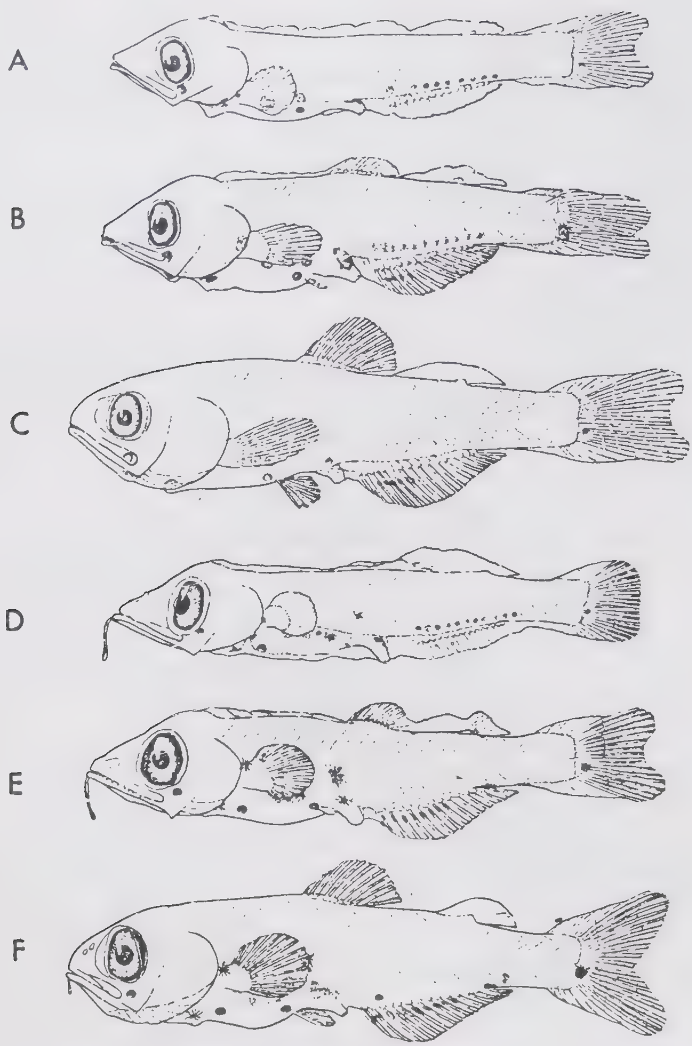

Figure 12. Larvae of myctophine lanternfishes. (A-C) *Diogenichthys laternatus*, 6.6, 7.7, 12.3 mm; (D-F) *Diogenichthys atlanticus*, 7.2, 8.8, 12.8 mm. From Moser and Ahlstrom (1970).

displacement of dorsal and anal fins. One could postulate hydrostatic (energy saving) or nutritional (energy storage) functions for these remarkable structures. These functions could be related to orienting/stabilizing and sensory functions for the elongate rays. Another possibility is that both the voluminous fin folds and the elongate trailing pectoral fin rays enhance the apparent size of the larvae and thus function as a deterrent to potential predators. The facts that the fin folds are emphasized by an even distribution of large melanophores and that the elongate pectoral rays are provided with large melanistic spatulations support this idea.

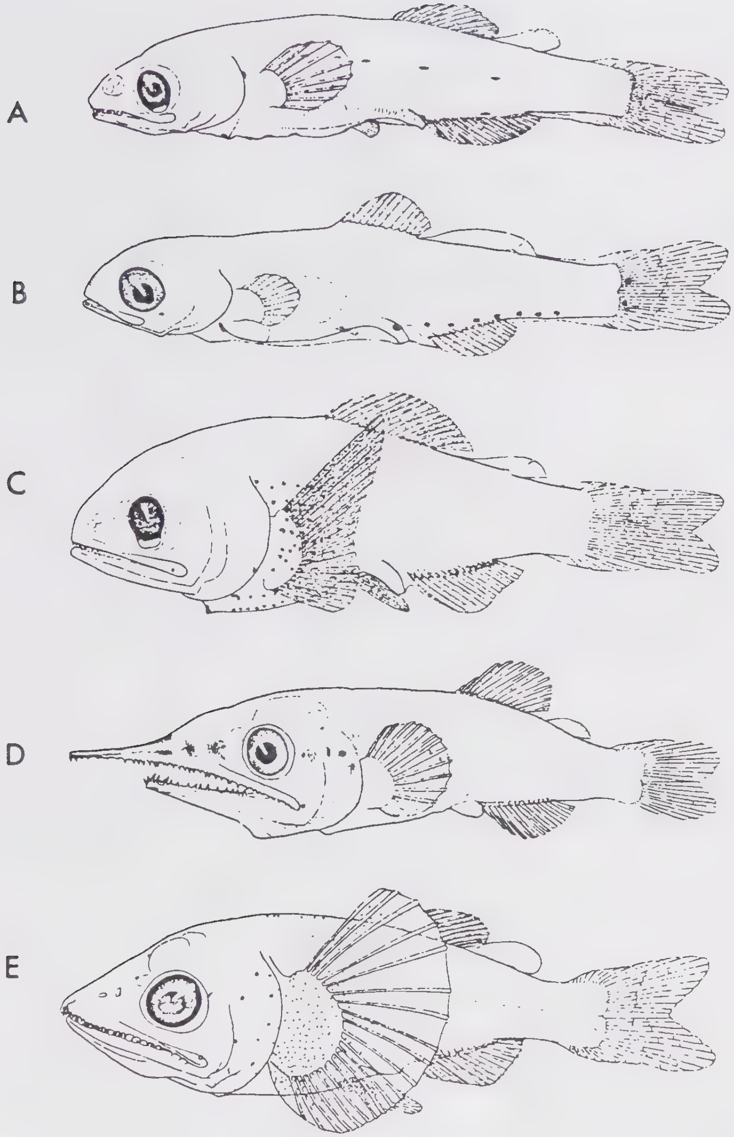

Figure 13. Larvae of lampanyctine lanternfishes. (A) *Triphoturus nigrescens*, 8.5 mm; (B) *Diaphus theta*, 6.9 mm, from Moser and Ahlstrom (1974); (C) *Lobianchia dofleini*, 8.2 mm, ibid; (D) *Lampanyctus achirus*, 13.4 mm, ibid; (E) *Lampanyctus sp.*, 9.4 mm.

Enlarged pectoral fins with supernumerary rays also occur in *Myctophum* and *Symbolophorus* and, in the other subfamily, have reached a peak of specialization in one group of *Lampanyctus* (Moser and Ahlstrom, 1974). In these species, fin enlargement is accompanied by increasing robustness of the body and prolongation of the extraordinarily toothy jaws, giving them a distinct predatory appearance (Fig. 13D, E). The body form of these larvae is

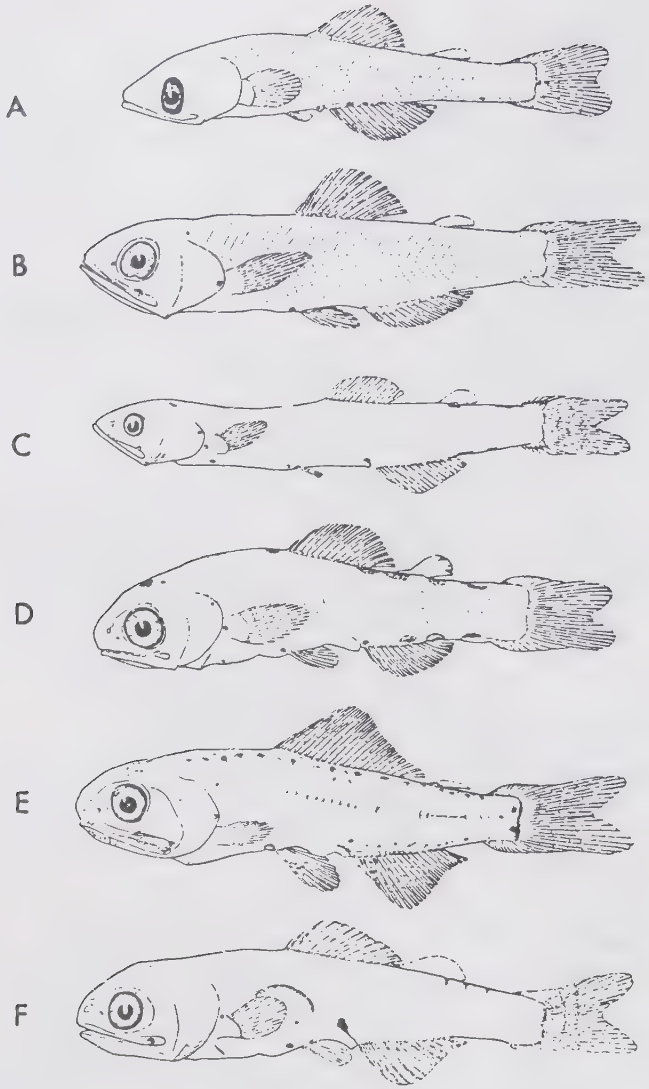

Figure 14. Larvae of notolychnine and gymnoscopeline lanternfishes. (A) *Notolychnus valdiviae*, 9.2 mm, from Moser and Ahlstrom, 1974; (B) *Ceratoscopelus townsendi*, 16.6 mm, ibid; (C) *Lepidophanes gaussi*, 13.5 mm, ibid; (D) *Lampadena urophaos*, 13.4 mm; (E) *Notoscopelus resplendens*, 16.2 mm; (F) *Lampanyctodes hectoris*, 11.7 mm, from Ahlstrom et al. (1976).

not commensurate with an S-shaped feeding strike, and one could speculate that pectoral fin thrust could play a part in the feeding strike. The "independence" of larval evolution is exemplified by these species when their robust, presumably motile and predatory larvae transform into soft-bodied, sluggish juveniles and adults. This is highlighted by the species with the largest larval pectoral fins, having the highest ray count of any myctophid, where the fin is lost completely in adults (Fig. 13E).

A major characteristic of gadiform larvae is a coiled gut, a feature found in larvae throughout the higher teleost groups. A coiled gut in the larval stage would appear to have certain advantages over the straight condition. By compressing the intestine in a mass behind the head, the digestive and propulsive systems become spatially separated and can specialize independently. Coiling would seem a natural prerequisite for the development of specialized digestive regions, separated by sphincters, that allow a more controlled rate of passage and digestion. A coiled gut with specialized functional regions is found in adults of most teleosts, whether or not their larvae have straight or coiled intestines. The development of the coiled specialized condition early in the ontogeny of most "advanced" teleosts appears to be a major evolutionary shift, permitting more efficient digestion and absorption and a greater variety of prey types.

In the gadoids, the cods and relatives, the larvae have large heads and jaws and an intestinal mass of large capacity (Fig. 15A–C). The ability of early larval stages to capture and retain prey items of a wide size range would seem advantageous to a group whose larvae are found typically in relatively deeper colder water (Sumida and Moser, 1980). In many species of morids, the pelvic fins appear early in the larval stage and develop elongate rays, sometimes ornamented with pigmented spatulations (Fig. 15E). Similarly, the macrurids develop large specialized pelvics, but also develop elongated dorsal rays and have curious paddle-shaped, highly peduncular pectoral fins (Fig. 16A).

Remarkable appendages are found in the larval stages of ophidioid fishes. Pearlfish larvae develop a highly modified dorsal appendage that bears leaf-like pigmented spatulations and in many species is directed anteriorly, possibly functioning as a lure (Fig. 16B).

What may be an example of mimicry is found in certain highly specialized ophidioid larvae that possess an ornate free trailing intestinal loop (Fig. 16C). Two such "exterilium" larvae have been reported, one taken in a trawl off Brazil (Nielsen, 1963) and the other captured alive after washing up on a beach near East London, South Africa (Fraser and Smith, 1974). A third specimen shown in Figure 16C was captured alive by a diver off New Guinea and deposited in the Scripps Institution of Oceanography Fish Collection (Cat. No. SIO 76–68). Although this larva is specifically distinct from the South African specimen (based on contrasting melanophore pattern, relative gut length, and other characters) both larvae have a fringe of fleshy cirri along the ventral edge of the intestinal loop and an arborescent appendage attached to the distal end of the loop. The cirri are marked with conspicuous large melanophores, and the resemblance of the entire structure to a siphonophore or other poisonous coelenterate prompted Fraser and Smith (1974) to suggest that the larvae may be discouraging potential predators through mimicry. One would associate such a large, highly specialized structure with prolonged pelagic life, and the authors may be correct in speculating that these are the larvae of some yet unknown group of slope or deep-sea ophidioids.

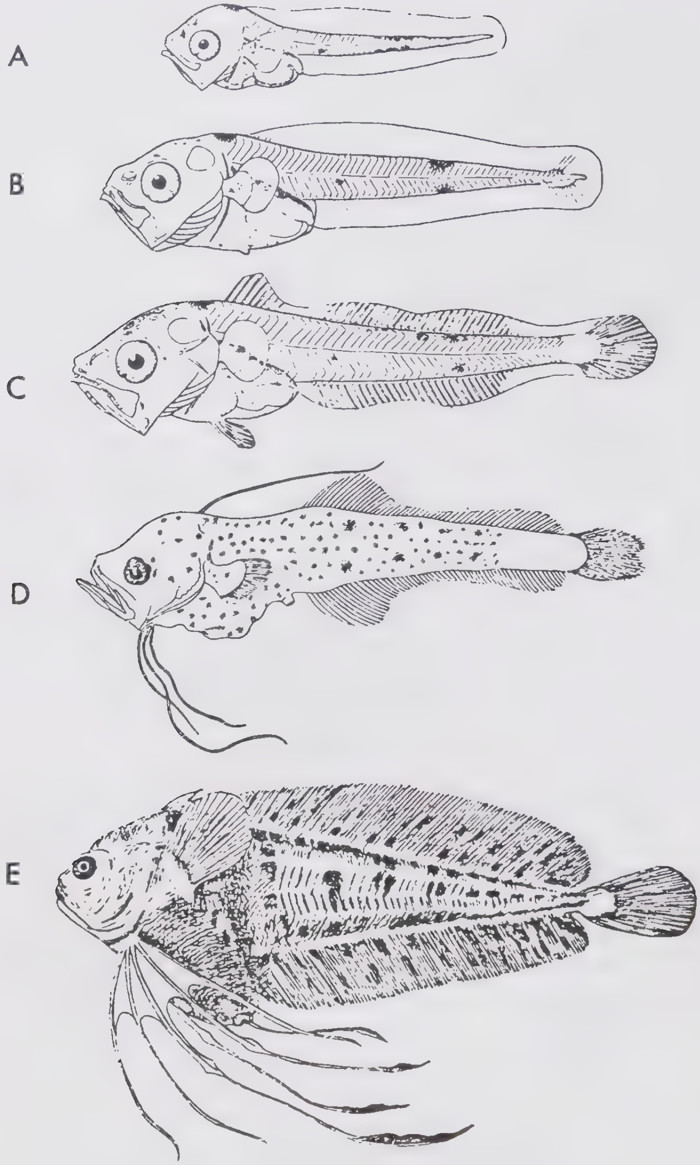

Figure 15. Young of gadiforms. (A-C) *Merluccius productus* larvae, 4.3, 7.7, 11.0 mm, from Ahlstrom and Counts (1955); (D) *Bregmaceros macclellandii* larvae, 10 mm, from D'Ancona and Cavinato (1965); (E) *Eretmophorus kleinbergi* pelagic juvenile, 105 mm, from D'Ancona (1933).

This remarkable adaptation probably arose secondarily from an adaptation associated with nourishment. Elongation of a straight intestine is common among salmoniforms and myctophiforms (Figs. 6, 11), presumably as an adaptation for improved digestion and absorption. Larvae of some higher teleosts have increased the gut mass by projecting an intestinal loop beyond the ventral body contour. This is particularly evident in bothid flatfishes such

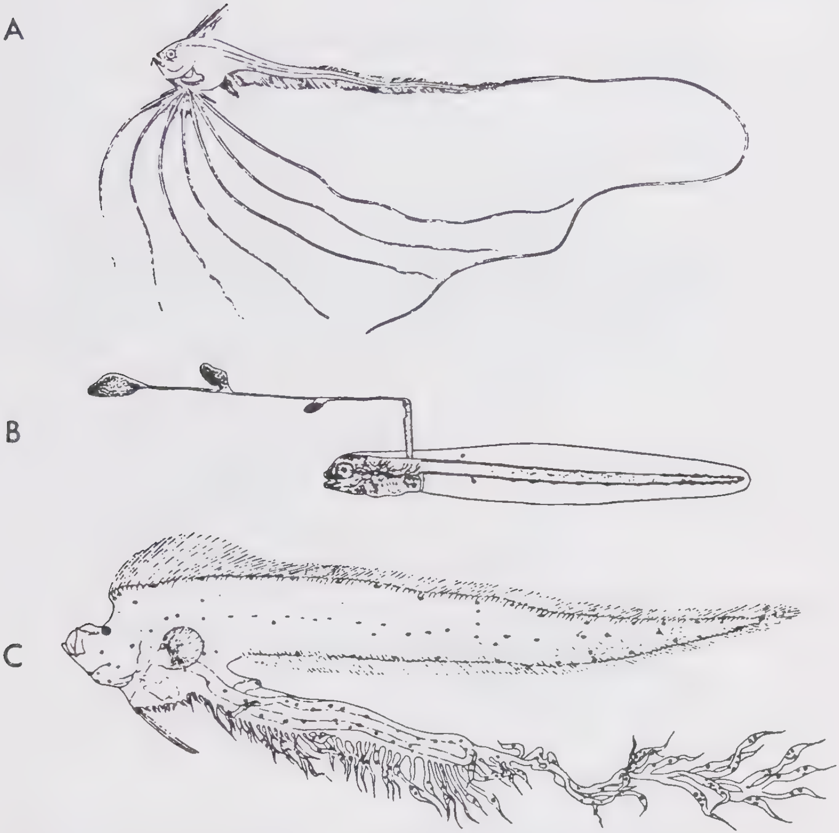

Figure 16. Young of gadiforms. (A) *Krohnius filamentosus* pelagic juvenile, 120 mm, from Sanzo (1933); (B) *Carapus acus* larva, 3.8 mm, from Padoa (1956); (C) exterilium larva, 64 mm, from Scripps Institution of Oceanography Fish Collection, Cat. No. SIO 76-68.

as *Laeops* (Amaoka, 1972) and in cynoglossid flatfishes. Presumably the trailing gut loop began as a nutritional adaptation in exterilium larvae and evolved through increasing levels of ornamentation to culminate in a structure of dual function.

Specialized elongate and often ornamented pelvic and dorsal fin rays are found widely among higher teleosts, particularly among the perciforms, pleuronectiforms, and lampridiforms. In the latter the character achieves its earliest ontogenetic expression (Figs. 17, 18). Lampridiforms produce large eggs, up to several millimeters in diameter, in which the larvae develop to an advanced state and form their elongate ornamented pelvic and anterior dorsal rays before hatching. The fact that enlarged specialized pelvic and anterior dorsal rays appear in larvae of many phylogenetically diverse higher teleosts speaks for the importance of these adaptations, whose possible functional significance was discussed earlier.

Another group with large eggs and advanced development before hatching are the atheriniform fishes—the flying fishes, sauries, and silversides. The eggs often have attachment filaments or spike-like processes, and the larvae

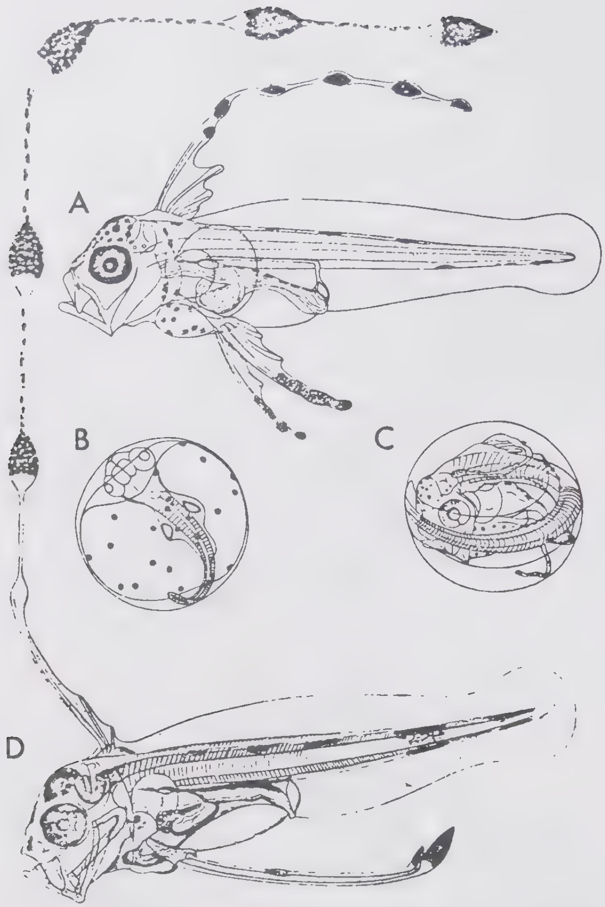

Figure 17. Larvae of lampridiforms. (A) *Trachipterus* sp., 7.6 mm, from Mito (1961); (B-C) *Trachipterus* sp., eggs, 1.8 mm, ibid; (D) *Lophotus* sp., 12.1 mm, from Sanzo (1940).

hatch with well-developed, highly functional pectoral fins and ontogenetically advanced and functional caudal fins (Fig. 19). The large egg, early fin development, and early-forming heavy melanistic pigmentation are adaptations to their stressful neustonic habitat that is characterized by high solar radiation, wind stress, and predation (by birds, invertebrates, and other fish).

The suggestion that ultraviolet radiation is the primary factor selecting for the heavy melanistic pigmentation found universally among neustonic fish larvae is supported indirectly by the experiments of John Hunter and his collaborators. Newly hatched anchovy larvae surviving four days of UV-B radiation equivalent to summertime levels off Southern California developed necrotic lesions of the eye and brain and had retarded growth and development (Hunter et al., 1979). Further experiments by Hunter et al. (in press)

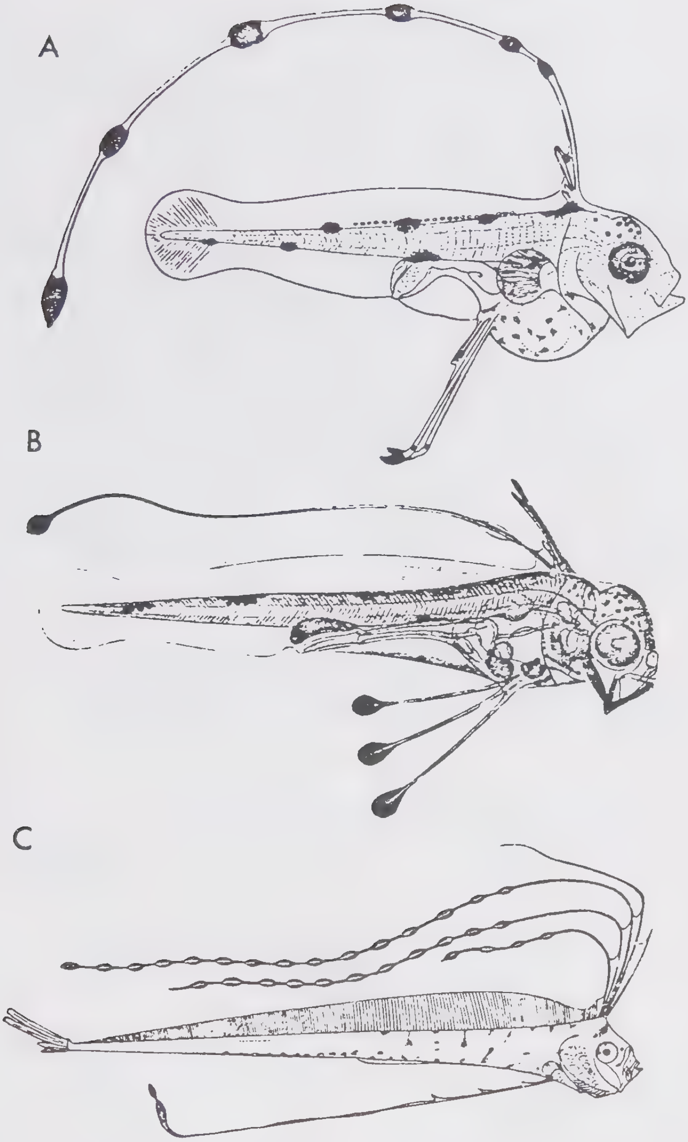

Figure 18. Larvae of lampridiforms. (A) *Zu cristatus*, 6.5 mm, from Sparta (1933a); (B-C) *Regalecus glesne*, 5.4, 45.8 mm, from Sparta (1933b).

show that developing anchovies are even more sensitive to a lower UV-B dose (equivalent to wintertime levels) given over a 12-day period, and place the LD_{50} depth at 4 m in clear oceanic water. (LD_{50} denotes the irradiation dose lethal to 50% of batch over a specified time interval.) Essentially UV-B radiation will not permit survival of the lightly pigmented anchovy larva at the surface off Southern California from March to October, while experiments on the more heavily pigmented robust larvae of Pacific mackerel show that they are twice as resistant to UV-B and could live at the surface year round.

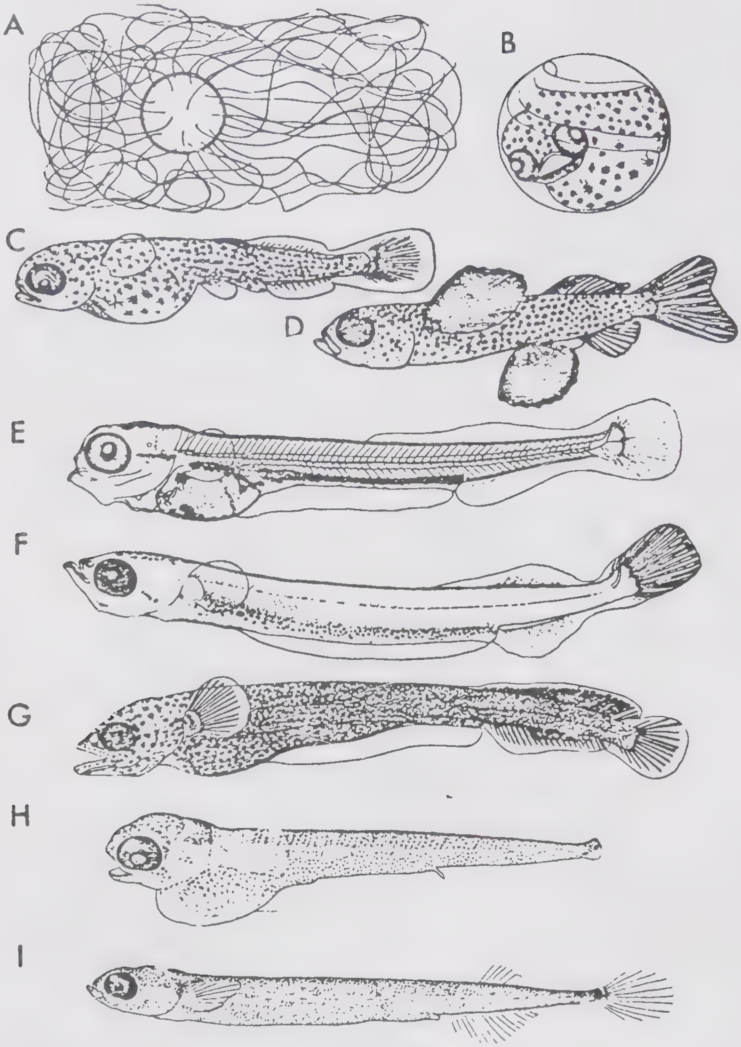

Figure 19. Larvae of atheriniforms. (A-D) *Cypselurus heterurus doderleini:* (A) egg with filaments, 1.9 mm diameter; (B) egg with 2-week-old embryo; (C) newly hatched larva, 6.3 mm; (D) 25-day-old larva, 14 mm, from Tsukahara et al. (1957); (E-F) *Hemirhamphus sajori*, 7.7 mm, 10.7 mm, from Uchida (1958); (G) *Tylosurus melanotus*, 10.2 mm, from Mito (1958); (H-I) *Cololabis saira*, 5.1, 9.9 mm.

Similar experiments have not been carried out on true neustonic species, those which live exclusively at the surface zone; however, the heavy melanism, whether it cloaks the body completely or is concentrated along the dorsum, provides protection from destructive effects of ultraviolet radiation. In addition to the heavy melanistic pigment, neustonic forms also have very heavy xanthic pigmentation that often takes the form of a solid yellow cloak and may provide additional protection from ultraviolet and visible light radiation. (For further discussion, see Perlmutter, 1961; Breder, 1962; Hempel and Weikert, 1972.)

What then is the major attraction of the neustonic zone? Zaitsev (1970) found relatively high concentrations of invertebrate plankters, of appropriate size for feeding larval fish, at the surface of the Black Sea. Similar studies yet to be carried out in oceanic waters may show that the neustonic zone is a kind of permanent food patch available to larval fish. Evolutionary requirements for successful exploitation of this "patch" appear to be a large, often attached, egg that permits advanced development before hatching, and a new-hatched larva that is relatively large, heavily pigmented, tough bodied, and capable of feeding and avoiding predators. That this neustonic morph has been achieved by species from so many phylogenetically divergent groups suggests a habitat of richness and complexity worthy of detailed study.

A major evolutionary theme in higher teleosts is spination. Within the dominant group of spiny-rayed teleosts, the Acanthopterygii, calcium metabolism and mobilization has reached a degree of perfection, and the array of fin spine, head spine, and dentitional arrangements is unmatched in complexity within the animal kingdom. The propensity to evolve specialized bony structures extends back into the larval period, where the diversity of fin and head spine specializations exceeds that of adult acanthopterygians (Figs. 20–26).

Primary sites for the accentuation and ornamentation of spines are at the anterior end of the dorsal and pelvic fins and on the head, usually posteriorly, where the head is widest and deepest, on bones such as the frontals, parietals, pterotics, posttemporals, preoperculars, and the opercular series (Figs. 20, 21). By having elongate fin and head spines at the widest region of the body the larva increases its size, from the standpoint of a potential predator, to a degree that is a function of spine length. Spines on the opercle can be extended laterally by flaring the gill covers to produce the same effect. The result is a prey item that is effectively larger, painful to ingest, thus more resistant to predation. Such a protective effect may be enormous at the size range of fish larvae, where small increments in actual or apparent prey size may have a disproportionately large effect in reducing predation by the smaller classes of organisms that prey on fish larvae.

Another effect of the elaboration of bony material into spines is to increase the specific gravity of the larva, thus posing a flotation problem. This is partially ameliorated in many larvae where structurally elegant spines are formed by supporting rods and thin serrated veins. Moreover, the center of gravity is shifted well forward in larvae with spiny heads. This appears to be compensated for in these larvae by a corresponding, more anteriad location of the gas bladder. Many acanthopterygian reef fishes (beryciform and perciform) produce larvae which inhabit open ocean waters and must have extended larval periods for their survival. They are among the spiniest of all fish larvae, leading to the often stated notion that spines enhance flotation. It is likely that increased spination in acanthopterygian fishes has the opposite effect and that flotation is the province of the gas bladder, even in fishes

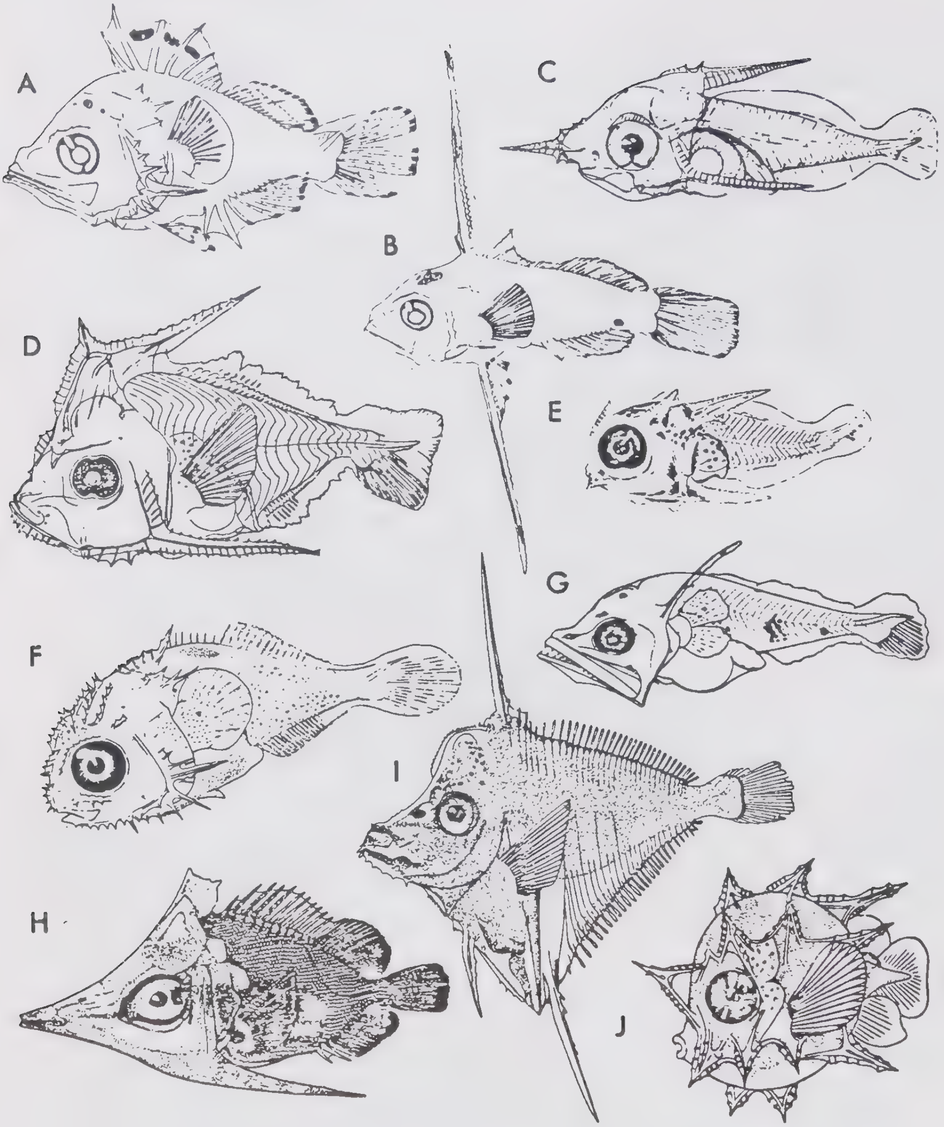

Figure 20. Larvae of acanthopterygii showing well-developed spination. (A) *Anthias gordensis*, 6.0 mm, from Kendall (1979); (B) *Epinephelus* sp., 8.4 mm, ibid; (C) *Holocentrus vexillarius*, 5.0 mm, from McKenney (1959); (D) *Antigonia rubescens*, 4.5 mm, from Uchida (1936); (E) *Dactylopterus volitans*, 3.5 mm, from Sanzo (1934); (F) *Caulolatilus princeps*, 6.0 mm; (G) *Champsodon snyderi* 4.6 mm, from Mito (1962); (H) *Forcipiger longirostris* (tholichthys stage), 17 mm, from Kendall and Goldsborough (1911); (I) acanthurid, 7 mm, from Weber (1913); (J) *Ranzania laevis*, 2.8 mm, from Tortonese (1956).

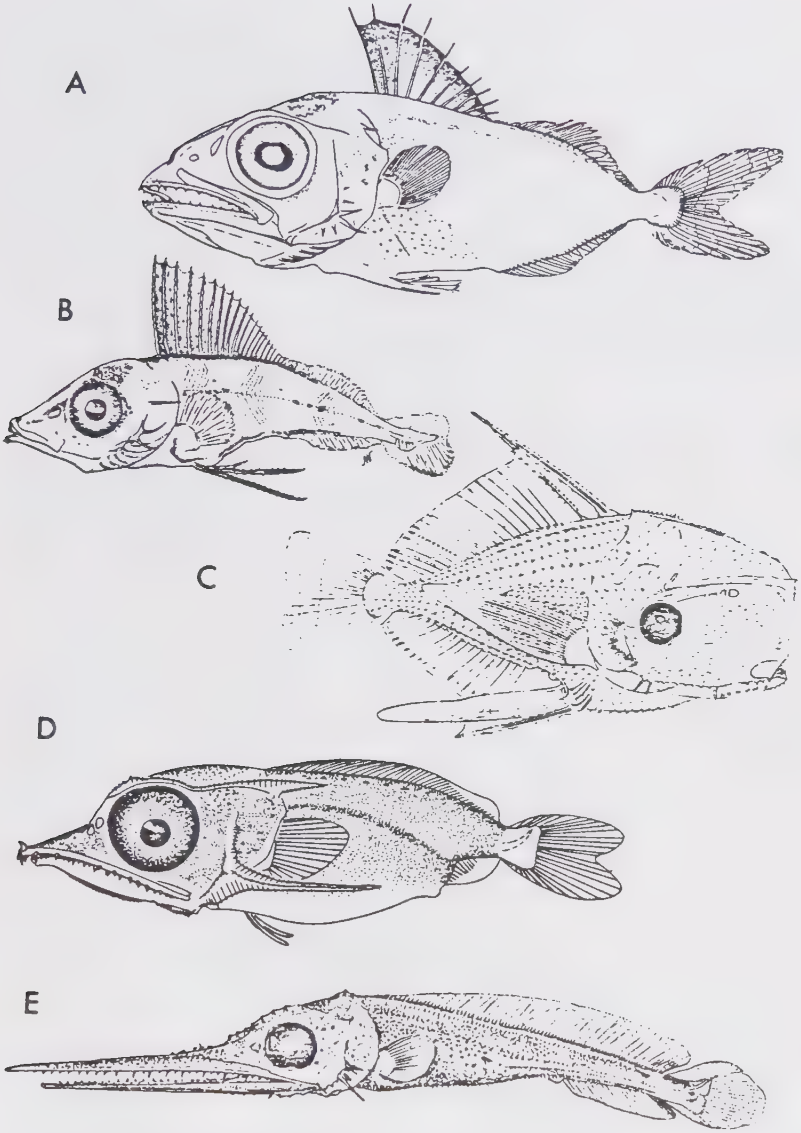

Figure 21. Larvae of scombroids. (A) *Thunnus albacares*, 14.2 mm, from Matsumoto (1958); (B) *Gempylus serpens*, 6.9 mm, from Voss (1954); (C) *Luvarus imperialis*, 11.9 mm, from De Gaetani (1930); (D) *Istiophorus americanus*, 8.1 mm, from Gehringer (1956); (E) *Xiphias gladius*, 15.6 mm, from Taning (1955).

where the bladder is lost during ontogeny. Voluminous finfolds (as in *Loweina*), distended gelatinous body envelopes (e.g., in lophiiforms and tetraodontiforms) and enlarged diaphanous fins may also serve to maintain buoyancy. It seems probable that the highly developed spination of many marine teleost larvae reflects the importance of predation as a major mortality factor during an extended larval period. In some reef and shore species a specialized pelagic juvenile stage is interposed between the larval and benthic juvenile stages. They have a unique morphology, with spines often accentuated beyond that of the larval period (Fig. 20H) and are capable of rapid transformation upon sensing bottom.

Although the adults of most spiny-rayed fishes are smooth-headed, the adults of some families within the acanthopterygian order Scorpaeniformes have complex and highly specific arrangements of head spines. Certain of these spines are well developed during the larval period and aid in identification, at least to the generic level (Moser et al., 1977; Richardson and Laroche, 1979). One group of scorpaenids, the rockfishes (*Sebastes* and relatives), have undergone extensive speciation in temperate and boreal waters. A major evolutionary trend in rockfishes is towards a more pelagic mode of life, with associated flexibility and streamlining of the body form, lightening of the skeleton, and reduction and loss of head spines. However, even the smooth-headed species have larvae with prominent head spines, many of which are lost gradually after the larval period (Moser, 1972; Moser and Ahlstrom, 1978; Richardson and Laroche, 1979; Laroche and Richardson, 1980). Retention of the ancestral pattern in their larvae suggests that the rockfishes are derived from warm-water benthic forms resembling the contemporary tropical genera, and also points out the ontogenetic and evolutionary plasticity of spine formation in this group (Moser and Ahlstrom, 1978).

Pigmentation has evolved to a high degree in larvae of acanthopterygians. In addition to the recurring types of melanistic pigment (e.g., gas bladder, oil globule, gut, post-anal series), whose possible functions were discussed earlier, unique melanopore patterns are found among the species of many groups. The possible role of pattern specificity in patch feeding was presented earlier. In addition to melanistic pigment, well-developed xanthic (yellow) pigment is encountered among the larvae of acanthopterygian fishes. The xanthophores may be in the same locations as the melanophores in a species, or they may be arranged in a distinctly different pattern, thus affording the larva two separate and unique patterns of pigmentation (see Mito, 1960, 1963, for examples). Where the xanthophores co-occur with the melanophores they may enhance the melanophore pattern signal, and where they are complementary they could serve to increase the specificity of the overall pattern. Xanthophore patterns seem to be best developed in coastal fishes, where reduced water clarity may obscure the melanistic pattern. An interesting feature of xanthophores is that they appear brown or black when viewed in transmitted light and have the appearance of melanophores when illuminated from the back. Much is to be learned about this dual capacity

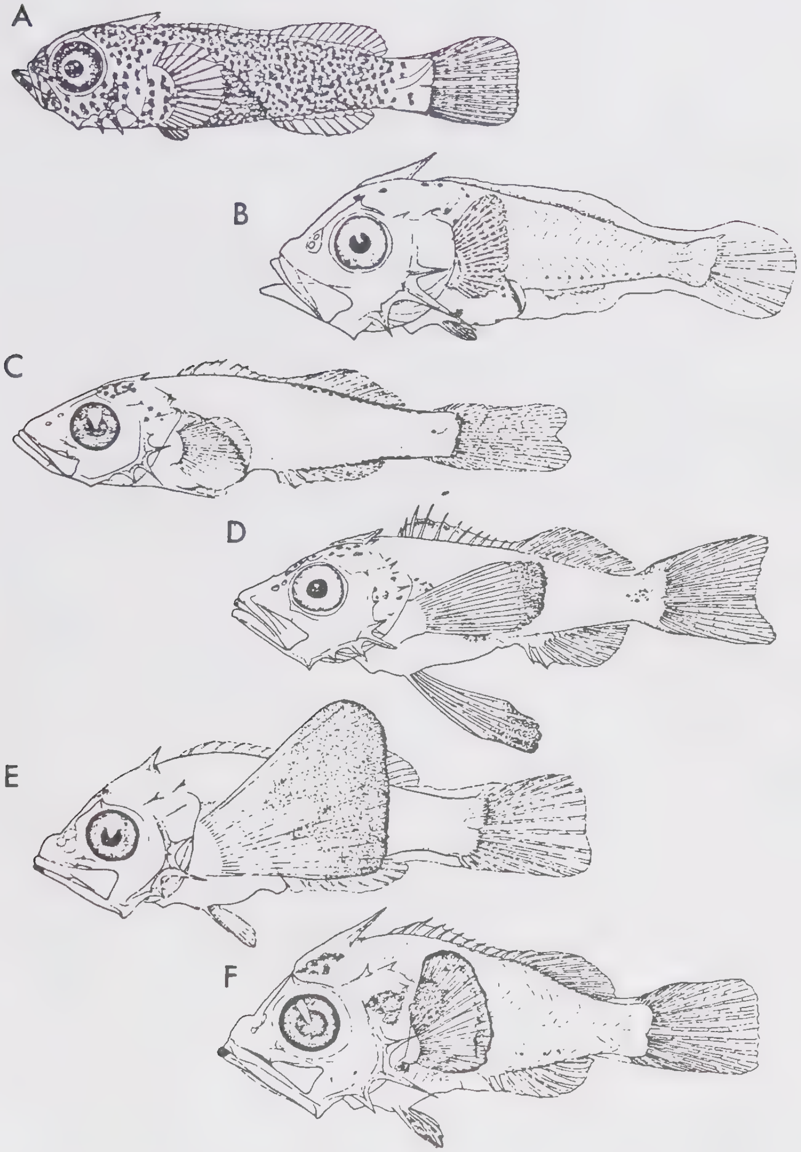

Figure 22. Larvae of *Sebastes*. (A) *S. oblongus*, 14 mm, from Fujita (1958); (B) *S. macdonaldi*, 9.0 mm, from Moser et al. (1977); (C) *S. jordani*, 15.5 mm, ibid; (D) *S. paucispinis*, 14.0 mm, ibid; (E) *S. levis*, 10.4 mm, ibid; (F) *S. melanostomus*, 8.2 mm, from Moser and Ahlstrom (1978).

and about the synthesis, arrangement, and role of xanthic pigment in fish larvae.

The flatfishes (Pleuronectiformes) are a large group of fishes which have become highly specialized for life on the seafloor and have both eyes on the side away from the substrate. In all flatfishes the eyes are symmetrical during the larval stage and migrate to their asymmetrical position during metamorphosis. In the pleuronectids (the highly successful group of northern seas) and the soleids (the true soles of temperate and tropical waters), the left eye migrates over to the right side of the head and the left side faces the substrate. The opposite is true for the diverse bothid and cynoglossid flatfishes of tropical and subtropical waters. Early in the larval stage, flatfish are not unlike larvae of typical acanthopterygians; however, they soon develop a deep, laterally compressed body form and a markedly coiled gut that is positioned well forward in the body.

Pleuronectiform larvae have a large array of morphological specializations (Figs. 24–26). The most prominent specialization is size. Size has played an important evolutionary role in larval flatfishes, perhaps more than in any other group of teleosts. To begin with, pleuronectiform eggs span the entire range of teleost egg size. Species with small eggs (ca. 0.6 mm in diameter), approaching the lower limit of teleost egg size, are found throughout the flatfish groups, and several species in the pleuronectid genera *Hippoglossus, Hippoglossoides*, and *Reinhardtius* approach the upper size limit for pelagic teleost eggs. Most notably, the eggs of the Greenland halibut, *Reinhardtius hippoglossoides*, are 4.0–4.5 mm in diameter and the larvae are 10–16 mm at hatching (Jensen, 1935).

The range of sizes encountered among flatfish larvae is greater than in any teleost group. Larvae of the achirine soles are among the smallest of all teleost larvae. For example, larvae of the lined sole, *Achirus lineatus* (Fig. 26), are 1.6 mm long at hatching and complete metamorphosis before they are 5.0 mm (Houde et al., 1970). In contrast, the larvae of some pleuronectids and bothids attain very large sizes (Figs. 24–25). Dover sole (*Microstomus pacificus*) larvae exceed 60 mm in length, and those of the rex sole (*Glyptocephalus zachirus*) reach a maximum of about 90 mm (Pearcy et al., 1977). Larvae of bothid genera such as *Kamoharaia, Laeops*, and *Taeniopsetta* reach sizes in the 70–90 mm size range, and those of *Chascanopsetta* exceed 100 mm (Nielsen, 1963; Amaoka, 1970, 1971, 1972). Barham (1966) observed from a submarine a remarkable bothid larva that he estimated to be more than 220 mm in length. The point is that, in flatfish, egg and larval size (and accordingly age) has been explored as a major adaptation.

Shallow or estuarine forms, such as the achirine soles, have solved the problem of recruitment of planktonic larvae to an areally limited bottom habitat by reducing the length and therefore the dispersal of the larval state. In contrast, the deepest living species have protracted the larval state through sustained growth, thus increasing the probability of settling success following shoreward and bottomward drift or migration. Not only is the time interval available for settling extended, but the length and time range over which metamorphosis can occur is increased in the species with larger larvae. This phenomenon is clearly demonstrated among the species of *Pleuronichthys* where there is a gradation in size at metamorphosis (Fig. 24). The bay and nearshore species transform and settle at small sizes, and the deeper water

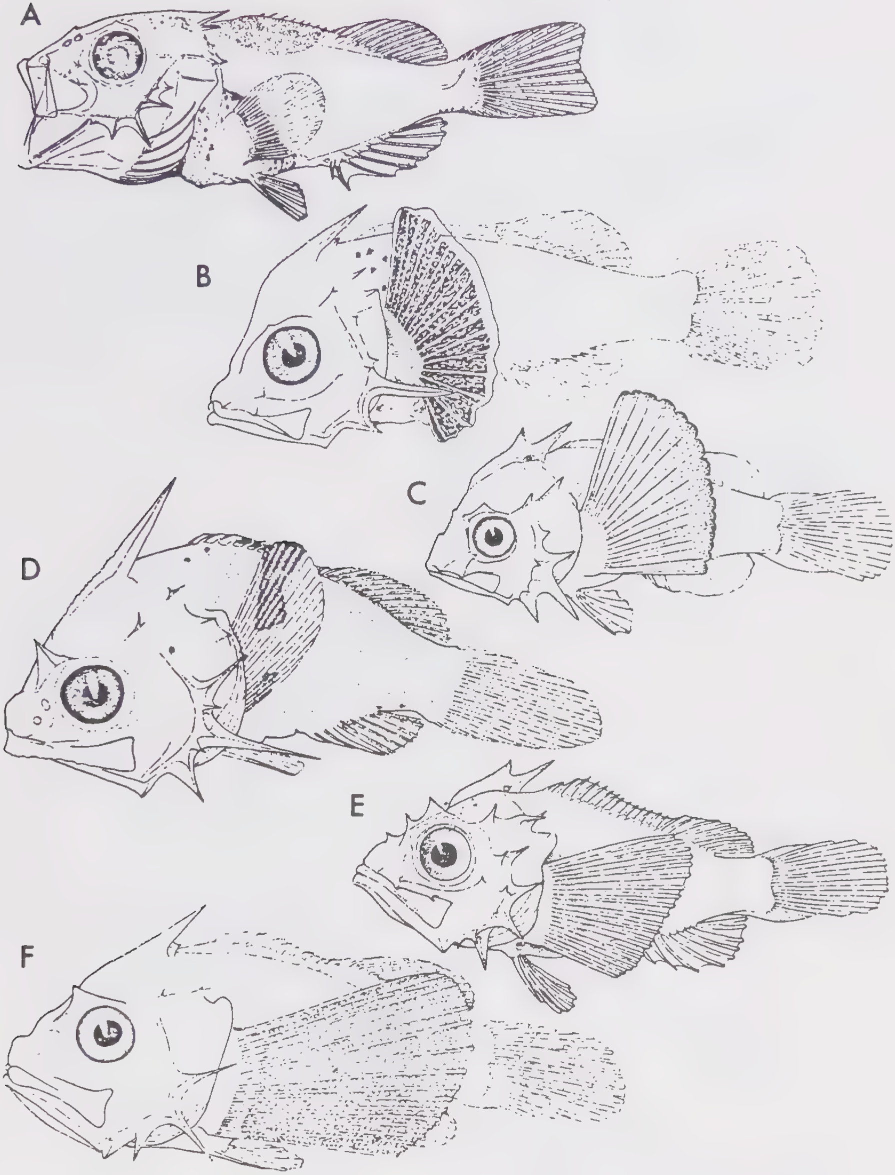

Figure 23. Larvae of scorpaenids. (A) *Helicolenus dactylopterus*, 19.0 mm, from Taning (1961); (B) *Scorpaena guttata*, 6.2 mm, from Moser et al. (1977); (C) *Scorpaenodes xyris*, 6.2 mm, ibid; (D) *Pontinus* sp., 5.0 mm, ibid; (E) *Sebastolobus altivelis*, 11.2 mm, ibid; (F) *Ectreposebastes imus*, 6.7 mm, ibid.

species attain larger sizes before metamorphosis (Sumida et al., 1979).

The heavily pigmented larvae of *Pleuronichthys* are taken frequently in our neuston collections. Particularly prominent in these collections are fully transformed juveniles of the deeper water species, *P. coenosus* and *P. decurrens*. Since transformed flatfish have a blind side, they would be at a disadvantage in finding food and avoiding predators prior to settling. These disadvantages might be reduced in the neustonic zone, where juvenile

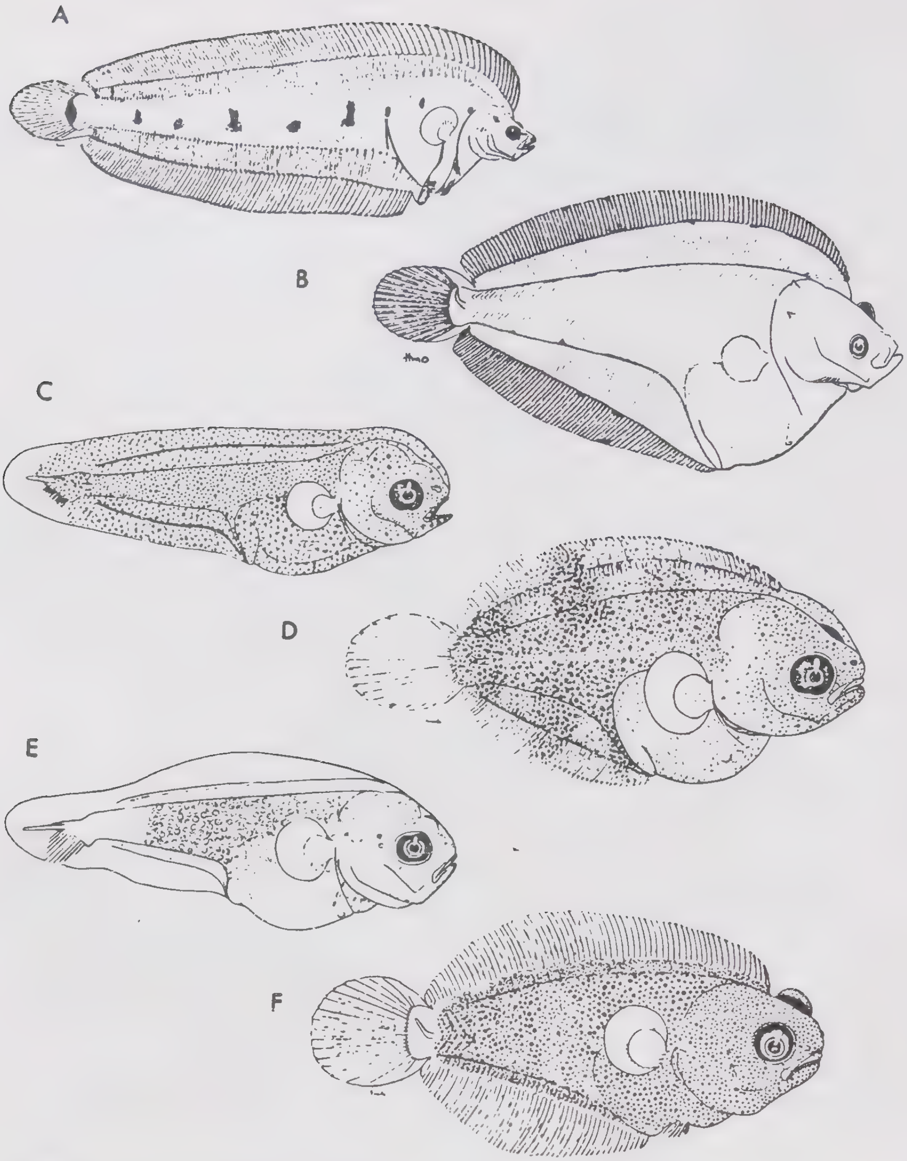

Figure 24. Larvae of pleuronectid flatfishes. (A) *Glyptocephalus zachirus*, 47.0 mm after Ahlstrom and Moser (1975); (B) *Microstomus pacificus*, 14.6 mm; (C) *Pleuronichthys decurrens*, 9.7 mm, from Sumida et al. (1979); (D) *P. decurrens*, 10.0 mm, showing initial eye migration, ibid; (E) *Pleuronichthys ritteri*, 5.6 mm, ibid; (F) *P. ritteri*, 6.4 mm, showing initial eye migration, ibid.

Pleuronichthys could feed efficiently on surface organisms while gaining some measure of disguise from their orientation just below the sea boundary. In effect, they may have "settled" temporarily at one surface before they arrive at water of appropriate depth for benthic settling.

The fact that flatfish species and genera with large larvae typically have broader zoogeographic distributions has led to the suggestion that increased

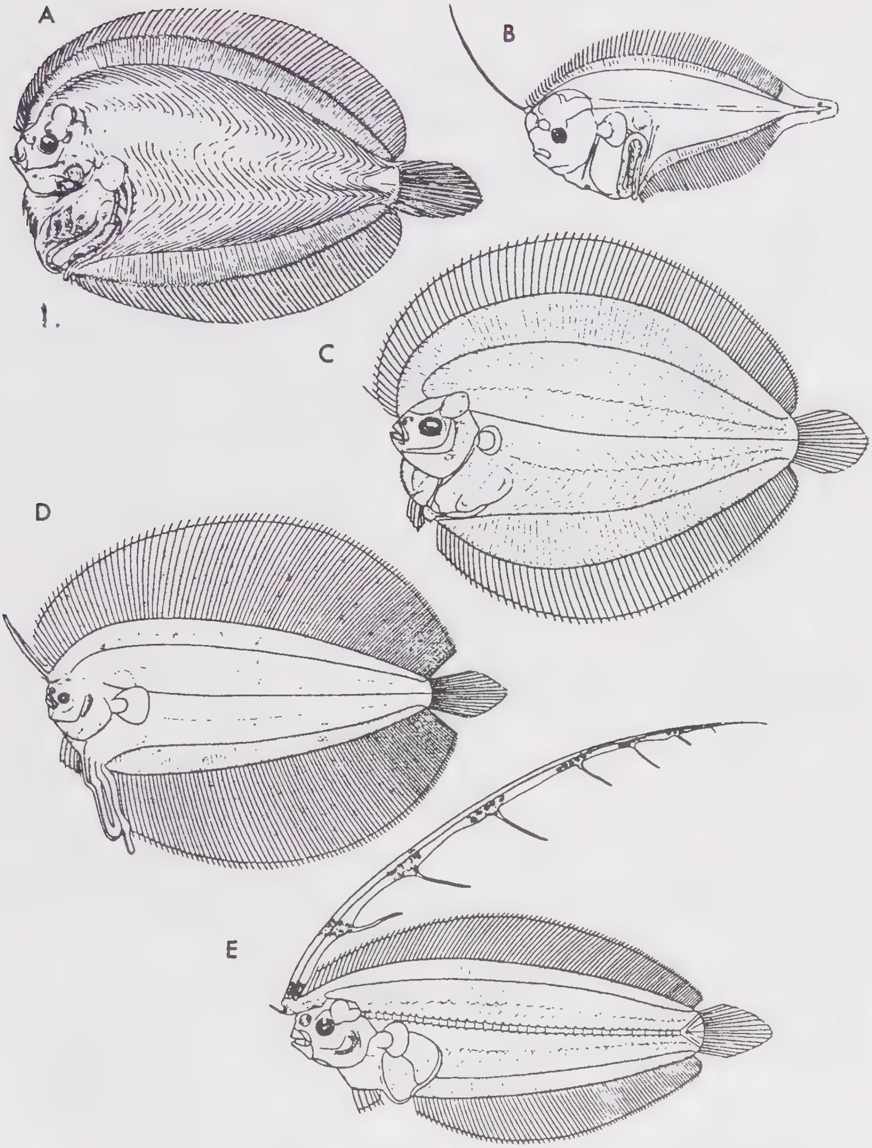

Figure 25. Larvae of bothid flatfishes. (A) *Bothus constellatus*, 27.1 mm; (B) *B. constellatus*, 6.2 mm; (C) *Taeniopsetta ocellata*, 59 mm, from Amaoka (1970); (D) *Laeops kitaharae*, 79 mm, from Amaoka (1972); (E) *Arnoglossus japonicus*, 30.5 mm, from Amaoka (1973).

size is a dispersal mechanism that increases species fitness (Brunn, 1937). An alternative hypothesis is that wide dispersal is a secondary consequence of increased larval size (and time) as a solution for the problem of larval settling in deep-living species.

The deep, sometimes leafshaped, body form of many larger flatfish larvae is related to a major locomotive adaptation. The deep body form results

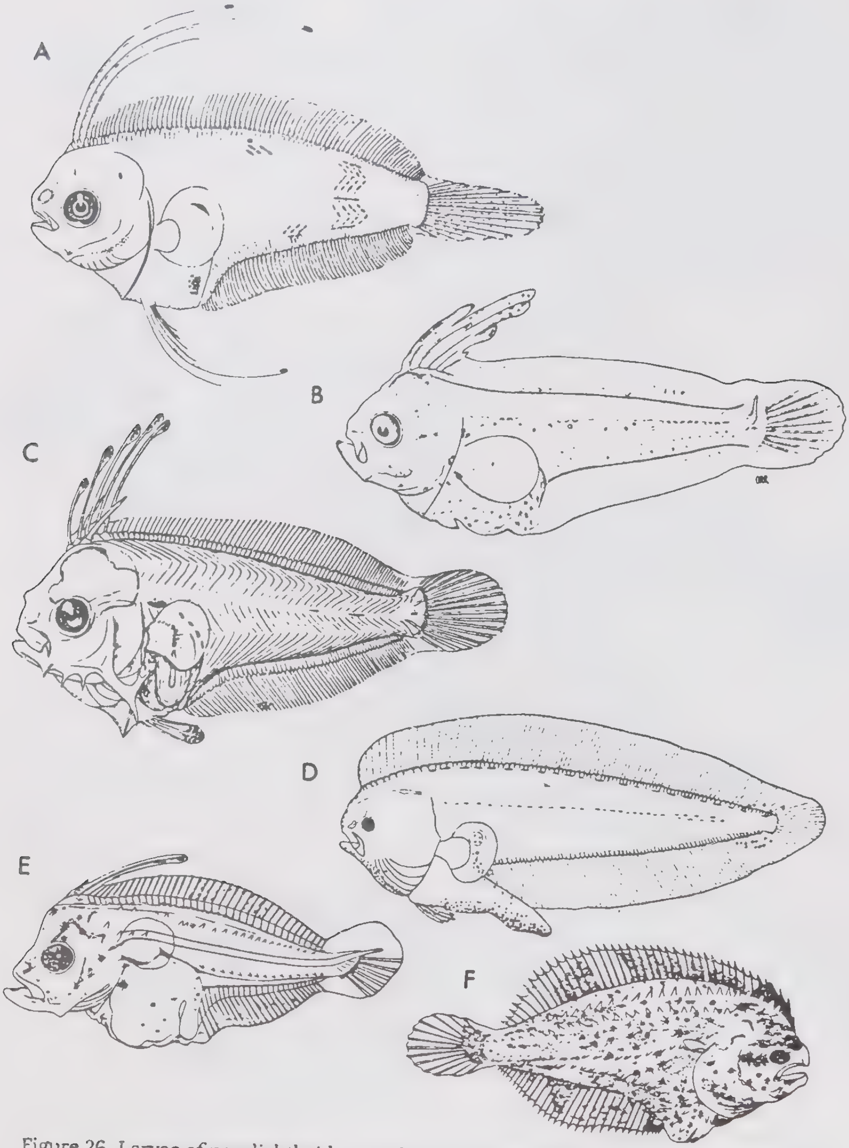

Figure 26. Larvae of paralichthyid, cynoglossid and soleid flatfishes. (A) *Citharichthys platophrys*, 8.6 mm; (B) *Paralichthys californicus*, 5.9 mm; (C) *Syacium ovale*, 6.5 mm; (D) *Symphurus atricauda*, 12.8 mm; (E) *Achirus lineatus*, 3.1 mm, from Houde et al. (1970); (F) *A. lineatus*, newly transformed specimen, 5.4 mm, ibid.

from the laterally compressed nature of the epaxial and hypaxial muscle masses, a widening of the dorsal and anal fin pterygiophore zones, and a lengthening of the dorsal and anal fin rays. The relative contribution of the pterygiophore zone to total body depth varies among species of flatfish. In some large deep-bodied larvae it contributes more to the total body depth than does the body musculature zone. Since flatfish larvae are extremely thin-bodied and flexible, the pterygiophore zone essentially enlarges the dorsal and anal fins, thus enhancing the power and precision of fin undulation. Barham's (1966) account of undulatory propulsion in the large unidentified flatfish larva and his estimate of 0.5 m/sec swimming speed highlight the importance of dorsal and anal fin undulation, with its associated enhanced directionality, in larval flatfish locomotion.

Further specialization of the dorsal fin is seen in bothid larvae (Fig. 25), which develop an elongate, sometimes ornamented, second dorsal ray and in many paralichthyid larvae (Fig. 26) which have a group of elongate anterior dorsal rays forming a comb-like structure. The elongate ray in bothids might have a sensory function. Barham (1966) observed that the dorsal fin "comb" was held erect during undulatory locomotion of his giant larva, and John Butler and I have observed that the smaller dorsal fin comb of reared California halibut (*Paralichthys californicus*) larvae is also held erect during locomotion, suggesting that the comb may function as a rudder during undulatory locomotion and possibly as a stabilizing vane during caudal-fin-generated feeding strikes. In some paralichthyid larvae, the pelvic fins are also enlarged by ray elongation and may function during undulatory locomotion.

Another possible function for the elongate dorsal ray in bothids and the elongate dorsal and pelvic rays in paralichthyids is to increase the apparent size of the larva as a means of reducing predation. In some species of the bothid genus *Arnoglossus* (Fig. 25E), the produced dorsal ray bears fleshy streamers and heavy pigmentation, and in paralichthyids such as *Citharichthys* and *Syacium* (Fig. 26A,C), the tips of the elongate dorsal and pelvic rays have pigmented spatulations. These highly emphasized rays produce the effect of a second body contour and thus may increase the apparent size of the larva, as suggested earlier in the lecture for groups with similar larval appendages.

Other specializations of flatfish larvae include a vast array of head spine patterns, the secondary elongation of the gut coil to a trailing condition in bothids and cynoglossids, and the development of highly complex and specific melanistic pigment patterns, particularly in the pleuronectids (Figs. 24–26).

One could not leave a survey of teleost larval specialization without mentioning the remarkable larvae of lophiiform angler fishes (Fig. 27). Goosefish (*Lophius*) larvae, with their elongate dorsal and pelvic fin rays, huge pectoral fins, balloon-like outer skin, and large size are among the most beautiful of all fish larvae (Fig. 27A). The adaptations are associated with prolonged pelagic life and presumably are related to the evolution of deeper-living benthic species, as suggested above for deep-water flatfish. Ontogeny in the deep-water pelagic angler fishes (Ceratioidei) is fully described in Bertelsen's (1951) definitive monograph. Dr. Richard Rosenblatt's suggestion (pers. comm.) that the deep water pelagic angler fishes are neotenic derivatives of benthic coastal forms via extended pelagic larval or juvenile stages is fascinating to consider; the gelatinous balloon-like skin of adult ceratioids

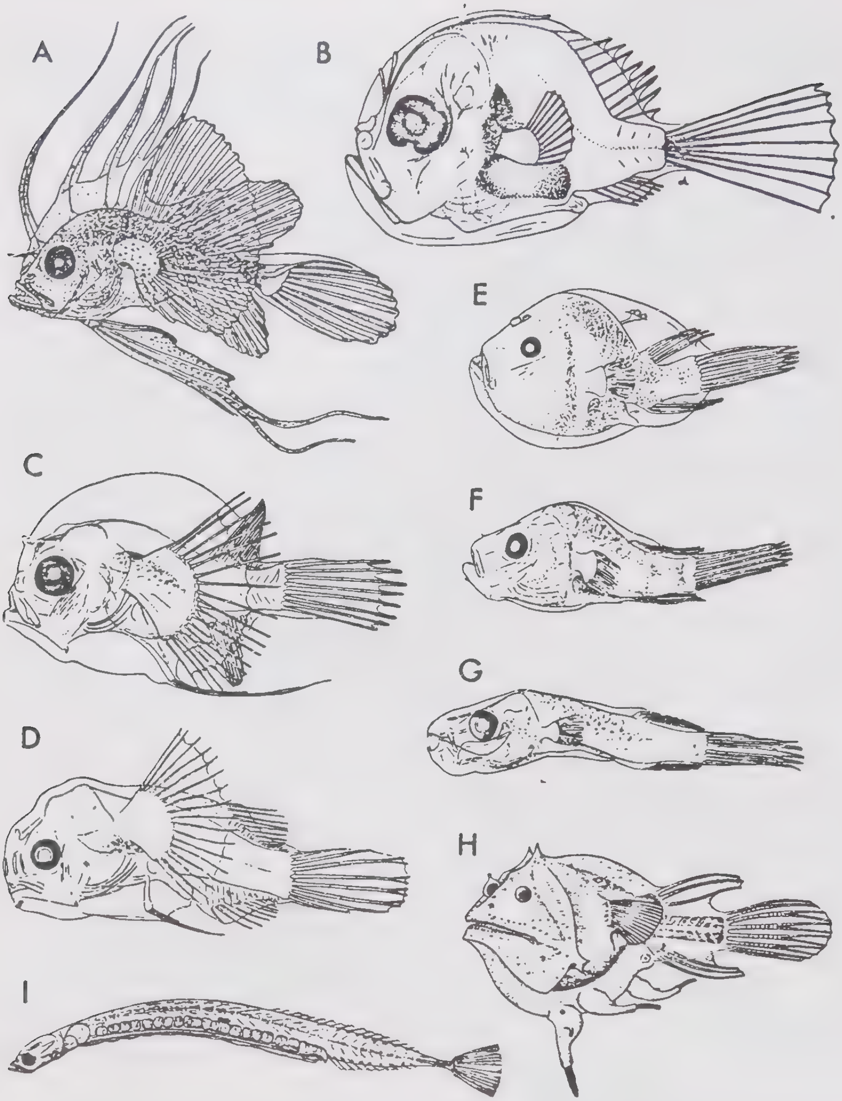

Figure 27. Larvae of lophiiforms and *Schindleria*. (A) *Lophius piscatorius*, 26 mm, from Taning (1923); (B) *Histrio histrio*, 2.0 mm, from Adams (1960); (C) *Caulophryne jordani*, 9.5 mm, from Bertelsen (1951); (D) *C. jordani*, 10.0-mm metamorphic male, ibid.; (E) *Cryptosaras couesi*, 11.8-mm female, ibid.; (F) *C. couesi*, 9.8-mm metamorphic male, ibid.; (G) *C. couesi*, 14.3 mm, oldest free-living stage of male, ibid.; (H) *Edriolychnus schmidti*, 70-mm adult female with 3 parasitic males, ibid.; (I) *Schindleria praematurus*, 15-mm ripe female, from Brunn (1940).

could be considered a retention of a pelagic larval character. The larvae of many ceratioids are sexually dimorphic and the mature males are distinctly larvoid in appearance. The reduction of ceratioid males to short-lived gamete carriers and the further reduction to attached "parasitic" sperm sacs in at least four families are well known. Larvoid males are also found in the stomiatoid, *Idiacanthus*, and the gobiid genus *Crystallogobius* appears neotenic. This tendency reaches the extreme in *Schindleria* (Fig. 27I), where adults range from 10.5 to 20.5 mm SL, weigh 2.0–8.0 mg, and in all appearances are larvae (Brunn, 1940). Here neoteny has been explored to the lower limits of vertebrate size and marks a convenient point to end the lecture.

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DESCRIPTION OF REARED LARVAE AND EARLY JUVENILES OF THE CALICO ROCKFISH, *SEBASTES DALLII*

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ABSTRACT

The developmental stages of the calico rockfish, *Sebastes dallii*, are described marking the first time that a species of eastern Pacific *Sebastes* has been reared from birth to pelagic juvenile. Larvae were obtained from a field-caught pregnant female and reared on wild zooplankton screened to a size range of 105-272 μm. Calico rockfish larvae are 5 mm long at birth and transform into pelagic juveniles by 20-mm length. The larvae are slender compared to those of most other described species and have a distinctive pattern of melanophores. Morphological and meristic features are described, with particular attention to the development of head spines. Rearing techniques are outlined and discussed.

RESUMEN

Se describen los estadíos de desarrollo de *Sebastes dallii*, marcando la primera vez que se haya cultivado una especie de *Sebastes* del Pacífico oriental desde el parto hasta la etapa de juvenil pelágico. Se obtuvieron larvas de una hembra capturada en su hábitat, y se alimentaron de zooplancton que se cirnió hasta obtener un rango de 105 a 272 μm. Las larvas de *Sebastes dallii* son 5 mm de largo al nacer y se convierten en juveniles pelágicos a los 20 mm de longitud. Estas larvas son más delgadas que las de la mayoría de otras especies descritas y tienen un patrón distintivo de melanóforos. Se describen sus características morfológicas y merísticas, con atención al desarrollo de las espinas de la cabeza. Se presentan y se discuten las técnicas de cultivo.

INTRODUCTION

Sebastes dallii is a small species of rockfish found in near coastal waters of 18- to 256-m depth from San Francisco, California, to Sebastian Viscaino Bay, Baja California (Miller and Lea 1972). It occurs in a variety of habitats from rocky reefs (Turner et al., 1969) to soft shelf substrates (Mearns 1979). Because of its small size and slow growth rate (Chen 1971), calico rockfish are not fished commercially and constitute a minor fraction of the sport fishery (Crooke 1978; Wine 1979). Mearns (1979), however, has shown that small juveniles of this species exhibit episodes of high recruitment to the coastal shelf of southern California, which suggests that they may be of ecological importance.

Sebastes dallii, like other species of *Sebastes*, is a fecund ovoviviparous fish whose larval stages are part of the ichthyoplankton. The larval and early juvenile stages of some *Sebastes* species have been described (Moser et al. 1977; Richardson and Laroche 1979; Laroche and Richardson 1980); however, little is known about the early life history stages of shallow-water coastal rockfish species. The difficulty in identifying larvae of nearshore fishes and the recent interest in coastal ichthyoplankton generated by environmental concerns stimulated us to rear larvae of these fishes to obtain voucher life history series. The life history series of *Sebastes dallii* described herein marks the first time a species of eastern Pacific rockfish has been reared from birth to juvenile.

MATERIALS AND METHODS

A pregnant 104-mm SL *Sebastes dallii* was collected by hook and line in shallow water south of the Coronado Islands, Baja California, on February 24, 1978. Larvae were freely running from the female at the time of capture. The larvae were immediately placed in 1-gallon jars of seawater where they began swimming towards the surface. The larvae were transported to the laboratory in an ice chest and placed in a 400-liter cylindrical black culture container within six hours of capture. At this time, some larvae appeared neutrally buoyant, as they maintained their position in the water column with little effort. Many larvae sank to the bottom, and mortality of these larvae over the next two days was probably 100%. The viable larvae had considerable amounts of yolk left, although not as much as those that sank to the bottom. Food was added to the cultures after four days in captivity. The food consisted of live plankton collected from Mission Bay, San Diego, with a 70-μm-mesh plankton net. The zooplankton was first screened through a 272-μm-mesh screen and collected on a 105-μm-mesh screen to select for smaller copepodites and nauplii. The initial densities of food organisms were copepods, 2/ml; copepodites, 4.6/ml; nauplii, 3.9/ml; polychaete larvae, 1.1/ml; and rotifers, 3.9/ml. A liter of a dense

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culture of algae, *Tetraselmis suesica*, was added daily as food for the zooplankton. The culture container was illuminated from above by four 40-W daylight fluorescent bulbs at 0.9 m from the surface. When the density of nauplii fell below 1/ml, additional zooplankton was added to the culture. As the larvae grew larger, larger zooplankton were added to the tanks. Moribund larvae and detritus were siphoned from the bottom of the container daily. Filtered seawater was added to maintain the culture volume at approximately 400 liters.

Larvae were removed from the culture tank over a period of 60 days and preserved in 4% buffered formaldehyde for subsequent analysis of morphometry and pigmentation and for meristic and osteological analysis. A series was cleared in a graded series of KOH-glycerin solutions and was stained with Alizarin Red-S. Terminology and methods of description follow those of Moser et al. (1977) and Moser and Ahlstrom (1978).

DESCRIPTION OF DEVELOPMENT

General Development

Larvae of *S. dallii* are released during winter and spring and are about 5.0 mm long at birth (Figure 1). Notochord flexion occurs between 6.2 and 8.0 mm, and the larvae have transformed into pelagic juveniles by 20.0 mm (Table 1). The larvae are comparatively slender with a relatively small head and large eyes. They develop a complex and distinctive pattern of melanophores (Figure 1) of which the postanal lateral series may prove to be diagnostic when the larvae of other nearshore species of *Sebastes* become known.

The slender terete pelagic juveniles (Figure 1E) resemble those of *S. jordani* in form and pigmentation (see Moser et al., 1977 for comparison). Mearns (1979) has shown that the juveniles become demersal in early summer at a length of 20-25 mm standard length (SL). A 36.6-mm benthic juvenile collected by otter trawl has the adult pigment pattern (see Phillips 1957).

Morphology

Larvae and pelagic juveniles of *S. dallii*, like those of *S. jordani*, are slender-bodied compared to other species (Table 2). Other features shared with *S. jordani* are a comparatively small head and short snout-to-anus distance. The latter character, of course, is not as marked as in the shortbelly rockfish, *S. jordani*. Eye diameter is greater in *S. dallii* than in the other species studied.

Spine formation in larvae of *S. dallii* (Table 3) follows in general the pattern described for other species (Moser 1972; Moser and Ahlstrom 1978; Richardson and Laroche 1979; Laroche and Richardson 1980). In *S. dallii*, the pterotics, 2nd and 4th anterior preoperculars, 1st and 4th upper infraorbitals, 1st lower infraorbital, lower posttemporals, and nuchals are present in larvae but are lost in subsequent juvenile stages. The cleithral spine is present in pelagic juveniles but becomes minute and finally lost in benthic juveniles.

TABLE 1

Measurements of Reared Larvae[1] of *Sebastes dallii*.

Standard length in mm (age in days)	Snout-anus distance	Head length	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Pelvic fin length	Snout-anal fin distance
5.1 (1)	2.2	1.1	0.21	0.45	1.0	0.29	0.16	—	—
5.3 (3)	2.2	1.2	0.35	0.45	1.0	0.29	0.25	—	—
5.4 (5)	2.3	1.2	0.31	0.43	1.0	0.28	0.35	—	—
5.5(11)	2.3	1.2	0.34	0.46	0.87	0.31	0.35	—	—
5.6(10)	2.4	1.2	0.31	0.46	0.85	0.33	0.35	—	—
5.7 (8)	2.4	1.3	0.33	0.51	0.96	0.34	0.42	—	—
5.9(10)	2.5	1.4	0.35	0.54	1.1	0.35	0.41	—	—
6.2(15)	2.6	1.5	0.40	0.53	1.0	0.34	0.46	—	—
6.5(32)	2.8	1.6	0.43	0.60	1.2	0.50	0.44	—	—
6.9(32)	3.1	1.8	0.57	0.65	1.4	0.52	0.63	0.02	—
7.0(32)	3.1	1.8	0.52	0.66	1.3	0.49	0.60	0.08	—
7.1(33)	3.3	1.9	0.55	0.73	1.5	0.54	0.59	0.10	—
7.3(33)	3.5	2.1	0.56	0.83	1.7	0.65	0.60	0.16	4.1
8.0(20)	3.8	2.1	0.58	0.79	1.8	0.61	0.70	0.13	4.4
7.3(38)	3.6	2.2	0.68	0.85	1.8	0.64	0.64	0.17	4.2
8.6(26)	4.2	2.4	0.72	0.88	1.9	0.70	0.83	0.22	4.8
9.4(28)	4.5	2.8	0.80	1.0	2.1	1.1	1.0	0.27	5.3
9.8(42)	5.1	3.2	1.0	1.1	2.2	1.2	1.0	0.34	5.7
10.1(49)	5.7	3.2	1.0	1.2	2.8	1.4	1.1	0.86	5.9
20.2(60)	11.7	6.1	2.0	2.1	5.1	4.7	1.7	3.3	12.3
21.7(60)	12.2	6.3	2.1	2.1	5.5	5.2	1.8	3.2	12.8

[1] Specimens between dashed lines are undergoing notochord flexion

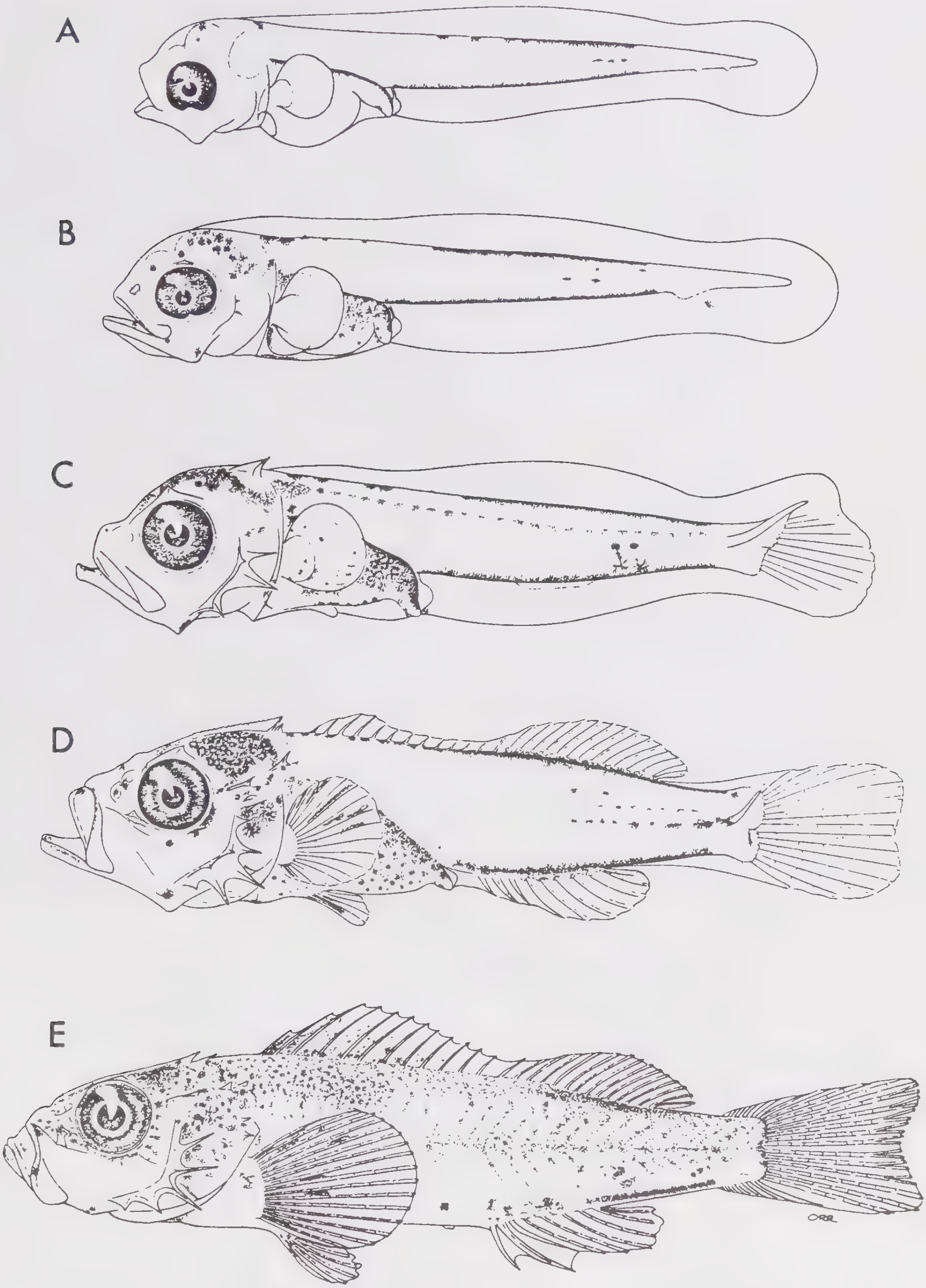

Figure 1. Reared specimens of *Sebastes dallii:* A. 5.1-mm larva (Day 1); B. 6.2-mm larva (Day 15); C. 7.1-mm larva (Day 33); D. 10.1-mm larva (Day 49); E. 21.7-mm pelagic juvenile (Day 60).

TABLE 2

Comparative Morphometry of Five Species of *Sebastes*[1]

Species		Snout to anus distance	Head length	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Pelvic fin length
		Body length	Body length	Head length	Head length	Body length	Body length	Body length	Body length
S dallii	A	42.4±0.52(42-43)	22.6±1.06(21-24)	25.6±3.02(19-29)	38.0±1.85(35-41)	17.6±1.85(15-20)	5.6±0.52(5- 6)	5.9±1.36(3- 7)	—
	B	45.7 2.07(43-48)	26.5 1.38(25-29)	28.7 1.86(27-32)	37.8 1.33(36-40)	20.7 2.07(18-23)	8.0 0.63(7- 9)	8.3 0.82(7- 9)	1.26±0.73(0.3-2)
	C	50.8 3.27(48-56)	30.6 1.95(28-33)	30.4 0.89(29-31)	36.8 1.92(34-39)	23.8 2.68(22-28)	11.0 2.45(9-14)	10.2 0.84(9-11)	4.0 2.83(2- 9)
	D	57.0 1.41(56-58)	29.5 0.71(29-30)	33.0 0.00(33)	33.5 0.71(33-34)	25.0 0.00(25)	23.5 0.71(23-24)	8.0 0.00(8)	15.5 0.71(15-16)
S jordani	A	36.5 0.84(36-38)	22.3 1.51(21-25)	26.8 3.43(23-31)	37.7 0.82(36-38)	17.0 1.26(16-19)	6.7 0.52(6- 7)	6.5 0.55(6- 7)	—
	B	42.4 1.67(41-45)	28.4 2.19(26-30)	35.5 1.29(34-37)	32.2 2.50(29-35)	2.10 1.00(20-22)	8.4 1.14(7-10)	7.8 0.45(7- 8)	1.4 0.55(1- 2)
	C	51.0 2.86(46-54)	32.3 1.44(31-36)	34.4 1.98(31-39)	29.3 2.10(27-34)	23.8 1.19(22-26)	16.8 3.25(11-20)	7.9 1.00(7-10)	9.0 3.62(3-13)
	D	53.3 1.03(52-55)	31.2 1.94(28-33)	34.0 2.83(30-38)	26.5 1.52(24-28)	22.2 0.84(21-23)	20.5 1.05(19-22)	7.0 0.00(7)	13.5 1.22(12-15)
S. levis	A	39.6 2.30(37-44)	24.7 1.60(23-28)	30.7 2.63(27-35)	33.1 2.67(29-36)	21.7 1.11(20-23)	17.4 5.29(11-24)	10.9 1.57(8-13)	—
	B	48.9 3.44(45-56)	30.5 1.85(28-33)	34.8 0.87(34-36)	32.5 1.77(30-35)	28.5 3.51(24-35)	34.9 6.96(24-46)	12.9 0.64(12-14)	6.1 3.27(2-12)
	C	59.2 2.87(57-63)	35.0 2.00(34-38)	30.2 2.22(28-33)	30.5 1.73(28-32)	34.0 1.41(33-36)	45.0 3.74(41-50)	11.2 0.96(10-12)	21.0 4.76(16-26)
	D	63.0 0.82(62-64)	33.8 0.96(33-35)	30.5 2.38(28-33)	27.0 3.37(25-32)	35.0 1.41(34-37)	40.8 7.09(32-47)	10.2 0.96(9-11)	24.2 2.87(22-28)
S macdonaldi	A	42.4 3.53(36-47)	27.6 2.25(24-31)	30.6 4.16(25-36)	34.6 2.34(31-37)	23.1 3.99(13-27)	8.4 1.21(6-10)	—	1.8 0.84(1- 3)
	B	51.8 3.56(48-56)	35.6 1.52(34-38)	34.0 4.00(30-38)	32.0 1.41(31-34)	31.6 2.07(30-35)	13.0 1.22(12-15)	—	5.8 2.39(3- 9)
	C	60.3 3.06(55-64)	37.5 1.84(34-41)	32.9 3.00(29-37)	33.0 1.33(31-35)	34.4 1.17(33-36)	19.3 3.65(15-26)	—	14.3 3.77(10-21)
	D	64.2 2.44(61-68)	35.1 2.37(32-38)	27.9 2.09(25-32)	30.7 2.74(26-34)	31.4 1.59(30-34)	30.4 1.74(28-34)	—	21.9 1.36(21-25)
S. paucispinis	A	41.0 2.74(37-44)	26.8 2.28(24-29)	27.4 3.21(24-32)	32.8 3.77(29-37)	19.6 1.67(17-21)	16.4 4.56(11-21)	9.0 0.71(8-10)	5.3 4.93(2-11)
	B	44.8 3.70(40-49)	29.6 1.95(27-32)	30.6 1.82(29-33)	30.2 1.64(29-33)	23.0 1.41(21-24)	27.2 2.49(25-31)	9.0 0.71(8-10)	13.6 9.28(9-26)
	C	57.3 3.82(51-61)	37.1 1.07(36-39)	32.2 0.98(31-33)	31.3 1.70(28-33)	29.6 0.98(28-31)	35.7 1.25(34-37)	7.6 0.53(7- 8)	35.1 2.79(31-39)
	D	62.3 2.73(60-66)	36.2 1.72(33-38)	30.5 2.95(26-33)	27.8 1.72(26-30)	27.3 0.52(27-28)	28.2 3.40(25-34)	6.0 0.89(5- 7)	25.2 2.71(22-30)

[1] A = preflexion larvae: B = larvae undergoing notochord flexion; C = postflexion larvae; D = pelagic juveniles

TABLE 3

Sequence of Development of Head Spines[1] of *Sebastes dallii*.

	Length of specimen (mm)															
Spine	5.6	5.9	6.0	6.3	6.4	7.1	7.3	8.0	8.6	9.8	10.1	20.2	36.6	49.1	53.0	67.5
Pterotic	X	—	—	—	—	—	—	—	—	—	—	—	—	0	0	0
2nd anterior preopercular	X	—	—	—	—	—	—	—	—	—	—	—	0	0	0	0
3rd posterior preopercular	X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Postocular		X	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2nd posterior preopercular				X	—	—	—	—	—	—	—	—	—	—	—	—
Parietal					X	—	—	—	—	—	—	—	—	—	—	—
4th anterior preopercular						X	—	—	—	—	—	0	0	0	0	0
4th posterior preopercular								X	—	—	—	—	—	—	—	—
Lower posttemporal									X	—	—	—	—	—	—	0
Lower opercular									X	—	—	—	—	—	—	—
Interopercular									X	—	—	—	—	—	—	—
1st upper infraorbital									X	—	—	0	0	0	0	0
3rd anterior preopercular									X/0	0	0	0	0	0	0	0
1st lower infraorbital										X	—	—	—	0	0	0
5th posterior preopercular										X	—	—	—	—	—	—
Nuchal											X	0	0	0	0	0
Upper opercular											X	—	—	—	—	—
Supracleithral											X	—	—	—	—	—
Nasal											X	—	—	—	—	—
Preocular											X	—	—	—	—	—
1st posterior preopercular											X	—	—	—	—	—
2nd lower infraorbital											X	—	—	—	—	—
4th upper infraorbital											X	—	0	0	0	0
Cleithral												X	—	—	—	—
Tympanic												X	—	—	—	—
Upper posttemporal												X	—	—	—	—
Subopercular													X	—	—	—

[1]Presence of spine is indicated by an "X" or continuous line. Absence of a spine is indicated by "0." In asymmetrical specimens, the condition of the left and right sides is separated by a slash.

The absence of supraocular and the 2nd and 3rd upper infraorbitals in larvae of *S. dallii* may be useful in identifying this species.

Fin Development

The pectoral fins of *S. dallii* larvae are the smallest of any species studied (Table 2; Richardson and Laroche 1979; Laroche and Richardson 1980). Rays begin ossifying at about 8.0 mm, and the full complement of 16-17 is present at 10.0 mm (Table 4). The pelvic fins begin to develop when the larvae reach 7.0-mm length, and they remain relatively small throughout the larval period (Table 2). Ossification of the rays begins in 9-mm larvae, and the full complement of I,5 rays is present at 10.1 mm. The cartilaginous radial elements and rays of the dorsal and anal fins appear in 7-mm larvae, and the ossification of the rays is initiated in 9-mm larvae. The 10-mm larva has

TABLE 4

Meristics of Cleared and Stained Larvae of *Sebastes dallii*.

Length (mm)	Principal caudal fin rays		Procurrent caudal fin rays		Branchiostegal rays		Pectoral fin rays		Hypural elements		Gill rakers (right arch)		Anal fin rays	Dorsal fin rays	Pelvic fin rays		Vertebrae
	superior	inferior	superior	inferior	left	right	left	right	superior	inferior	upper limb	lower limb			left	right	
5.9					1	1											
6.0					1	1											
6.2	1	1			2	2											
6.4	2	3			2	2											
7.1	3	4			3	3											2
7.3	4	4			4	4											2
8.0	7	8			6	6	7	7	1	2		10					20
8.6	8	7		2	7	7	11	11	1	2		12					23
9.8	8	7	3	4	7	7	15	15	1	2		14	II,6	IV,11	I,2	I,2	26
10.1	8	7	7	8	7	7	17	18	1	2	4	17	III,6	XIII,13	I,5	I,5	26
20.2	8	7	12	13	7	7	17	17	2	2	9	22	III,6	XIII,13	I,5	I,5	26

the adult complement of XIII, 13 dorsal and III,6 anal rays.

The caudal fin begins to form at about 6.0 mm with the appearance of some cartilaginous hypurals and principal rays. Ossification of the principal and procurrent rays is shown in Table 4. As described for *S. melanostomus*, the lowermost superior hypural and the uppermost inferior hypural each have two centers of ossification, which may relect the ancestral condition of 3+3 hypurals in the family (Moser and Ahlstrom 1978).

Pigmentation

The pigment pattern of newborn larvae consists of a postanal series of melanophores along the dorsal and ventral midlines, a short postanal series along the horizontal myosepta, one to several spots at the nape, a patch of melanophores above the brain, an embedded melanophore in each otic region, and a series of melanophores along the dorsolateral surfaces of the gut on each side (Figure 1A).

For 50 newborn larvae the number of melanophores in the ventral postanal series ranged from 29 to 49 ($\bar{x}$ = 37.7 ± 4.33 SD), whereas the number in the dorsal series ranged from 7 to 19 ($\bar{x}$ = 13.7 ± 2.74 SD). The ventral series extended from the first to the 15th or 16th postanal myomere, and the dorsal series extended from the 4th or 5th to the 14th or 15th postanal myomere. The lateral postanal melanophores ranged from 1 to 6 ($\bar{x}$ = 2.3 ± 1.20 SD) on the left side and 0 to 5 ($\bar{x}$ = 1.8 ± 1.13 SD) on the right side. Four specimens lacked lateral melanophores on the right side.

Melanophores above the brain ranged from 1 to 9 ($\bar{x}$ = 4.2 ± 1.79 SD) whereas those on the nape ranged from 0 to 6 ($\bar{x}$ = 2.0 ± 1.17 SD). Two specimens lacked nape melanophores. Of the 50 specimens, 12 had otic melanophores on both sides, 14 lacked them on one side, and 24 lacked them on both sides.

The ventral postanal series remains throughout the larval period, but becomes divided into two lines on either side of the developing anal fin in 7-mm larvae. Anterior to the anal fin, the two lines become embedded and extend anterior to the anus. In some larvae, one to several melanophores may form just lateral to the posterior region of the ventral midline series. They appear in 80% of the specimens from 6.2 to 10.1 mm and, when maximally developed, appear as a bridge between the ventral midline series and the series along the horizontal septa (Figure 1C).

Melanophores are added anteriorly to the dorsal midline series and reach the level of the anus when the larvae are about 6.0 mm (Figure 1B). Thereafter, melanophores are added irregularly in the zone between the occiput and the anterior end of the dorsal midline series. These melanophores form in two lines on either side of the dorsal midline. When the dorsal fin begins to form in 7-mm larvae, the postanal dorsal midline series begins to separate into two series on either side of the midline, and these become continuous with the more anterior dorsal pigment lines. The smallest specimen in which the dorsal pigment is continuous from occiput to caudal peduncle is 7.3 mm.

The lateral postanal melanophores persist throughout the larval period. For 37 specimens between 5.0 and 8.0 mm, the number of lateral melanophores on the left side ranged from 0 to 7 ($\bar{x}$ = 2.5 ± 1.43 SD), and those on the right side ranged from 0 to 5 ($\bar{x}$ = 2.6 ±1.26 SD). Of the 37 specimens, only four lacked lateral melanophores on one side, and all had them on at least one side. Melanophores are added to the lateral series in larger larvae, and in the two pelagic juveniles the entire horizontal myoseptum is heavily pigmented, as are the myosepta above and below it. A zone of solid pigmentation covers the dorsal region of the body (Figure 1E).

Melanophores are added to the patch above the nape so that the entire nape is covered when the larvae reach 6.0 mm (Figure 1B). At this size the patch begins to be overlain by dorsal musculature, and simultaneously, embedded melanophores begin to appear over the posterior region of the vertebral column. Melanophores are added between this region and the embedded nape patch, and in larvae as small as 6.9 mm, the series of embedded melanophores above the vertebral column is complete (Figure 1C).

Melanophores are added above the brain so that in 6-mm larvae, where there are 12-14 melanophores, the dorsal surfaces of the optic and cerebellar lobes are solidly pigmented. Melanophores also begin to appear on the lateral and ventrolateral surfaces of the cerebellar and medullary regions, and by 7.0 mm these areas are solidly pigmented (Figure 1C). Melanophores appear on the dorsal surface of the olfactory lobes at about 5.5 mm and number from 1 to 3 until the larvae reach 7.0 mm, when the region becomes solidly pigmented.

Melanophores appear on the lower jaw in larvae about 5.5 mm long. One to several melanophores are present anteriorly on one or both sides of the jaw in about half the larvae up to 7.0 mm. More are added in larger larvae to cover the anterior curve of the lower jaw (Figure 1D). Melanophores also form posteriorly on the jaw. One or two may be present on each side in the region of the articular bone, and one or two may form in the angular region. Melanophores may be absent in either the angular or articular region on either side, but at least one melanophore is present on the posterior lower jaw.

At about 7.0 mm, melanophores appear at the anterior region of the snout. In about half the larvae larger than 7.0 mm, one or two melanophores are present in the midline of the snout between the maxillaries. From one to three melanophores may form along the maxillaries lateral to the median snout region, with about half the specimens lacking them altogether on one or both sides. More appear at about 10.0 mm to form a streak along the upper portion of each maxillary (Figure 1D). Also, in 7-mm larvae, one or two melanophores may be present on each nasal flap. In larvae of about 10.0 mm, the nasal flaps become solidly pigmented. In larvae larger than 7.0 mm, one to several melanophores are usually present on the upper region of the opercle (Figure 1C) along with a single melanophore on the preopercle posterior to the eye. Melanophores in these regions increase in number at about 10.0 mm, and the entire upper half of the head is pigmented in the pelagic juveniles (Figure 1D, E).

The initial melanophore pattern of the gut region is augmented in larvae between 5.0 and 6.0 mm. The dorsolateral gut pigment increases to form a shield over the gut (Figure 1B). Also, pigment extends forward internally to form an embedded melanistic zone medial to the cleithra. On the ventral midline of the gut a preanal and cleithral melanophore are at each end of a series that can range up to 10 in number. When expanded they appear as a partial or complete line. In later stage larvae the dorsolateral shield extends ventrad and reaches the ventral midline in larvae larger than 8.0 mm.

The fins are lightly pigmented. The first pigment to form is a single melanophore in the future hypural region of the developing caudal fin (Figure 1B). It is present in about one third of the larvae larger than 5.2 mm. When the hypurals begin to develop, the melanophore is usually located at the posterior margin of the hypural plate between the superior and inferior groups of elements. At about 10.0 mm, additional melanophores form along the posterior margin of the plate and outline the entire posterior margin in the pelagic juveniles. Pigment appears on the pectoral fins in some 7-mm larvae, where one to several melanophores may be present on the dorsal and on the ventral region of the blade (Figure 1C). A maximum of 7 upper and 4 lower melanophores is present in larvae up to 10 mm and a maximum of 12 was present on the fin blades of the pelagic juveniles. A patch of melanophores begins to form on the medial surface of the pectoral base in 8-mm larvae and intensifies with development. Pigmentation first appears on the pelvic fins in 8-mm larvae as a melanophore at the base and one to several on the fin blade. Melanophores are added to the blade in later stages but are restricted to the proximal region (Figure 1C). Pigmentation is present on the spinous dorsal fin in the two pelagic juveniles. The first two interradial membranes of the spinous dorsal are solidly pigmented, and the membranes between the 3rd and 10th spinous rays have scattered pigmentation restricted to the proximal half of the fin (Figure 1E).

DISCUSSION

Although Japanese workers have successfully reared four species of western Pacific *Sebastes* (summarized in Moser et al. 1977), *S. dallii* is the first eastern Pacific species to be reared through to juveniles. Reasons for our previous lack of success in rearing larvae of several *Sebastes* species using a diet of *Artemia* nauplii (as used by the Japanese workers) and more recently a diet of the rotifer, *Brachionus plicatilis*, are open to speculation. One possibility is that *S. dallii*, being a moderately shallow species, has more robust larvae than those of the deeper water species used in previous rearing attempts. The four successfully reared western Pacific species are all shallow-water forms (Lo-chai Chen, personal communication). Also, the diet of wild zooplankton maintained at high densities during the first few days of feeding undoubtedly contributed to our success. *Artemia* nauplii are far from an optimally nutritional diet, and our experience with *Brachionus* was that even high densities of this organism did not elicit a feeding response in rockfish larvae.

Perhaps the most important factor in achieving success with *Sebastes* larvae is the stage of development at birth. Timing of birth in the wild appears to be precisely related to stage of development, perhaps by some biochemical or mechanical cue from the larvae, and capture of full-term females that are ready to give birth is a rare event. This raises the more general question of whether or not there is a maternal nutritional contribution in addition to the yolk. If this were true, one might speculate that such nutrition is critical to development of certain organ systems late in the pregnancy and that premature birth might impair organogenesis. Affirmation of this speculation must await future physiologial studies on intraovarian development of *Sebastes*.

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Development of Organ Systems in the Northern Anchovy, *Engraulis mordax*, and Other Teleosts[1]

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SYNOPSIS. Certain aspects of development that are indicative of changing functional and ecological capabilities are reviewed for six different organ systems in the northern anchovy, *Engraulis mordax*, and other teleosts. The six organ systems are the integument, the lateral line system, the eye, the digestive tract, the gas bladder, and the trunk musculature. The integument develops gradually but also has transient specialized cells during the larval period. The lateral line system is functional at hatching and then elaborates by recruitment proportional to growth during the larval period. The eyes are capable of photopic binocular vision when feeding starts, and later gradually develop a scotopic system. The digestive tract develops a capacity for protein digestion and filtering during the mid and late larval period. The gas bladder gradually develops an expansion capability by muscle differentiation after initial inflation. The trunk musculature differentiates and recruits two fiber types that gradually supercede the embryonic musculature during the larval period. Thus much of the development of organs in the anchovy after hatching or after feeding starts can be characterized as initial differentiation and then continued recruitment of specialized cell arrays. Behavior patterns appear to develop in conjunction with such recruitments. This may apply to fishes generally, but pattern and tempo of development must differ among species. Brief comparison of the anchovy and the Pacific mackerel, which has a more rapid and direct development, suggests that some of the differences in the two types of larvae relate to the marked difference in feeding modes of the adult stages.

INTRODUCTION

In teleost fishes that hatch from pelagic eggs in the sea most organ systems originate in the late embryonic period or the larval yolk sac stage, and become functional by the end of this stage. The yolk sac stage lasts for a few days to a week, depending on temperature, and when yolk is gone the larvae must start feeding. As they grow during the ensuing larval period, nutritional demand increases continually, and feeding habits, locomotor patterns and other ecological characteristics change. The maturation of organ systems that occurs over the larval period must involve capacity and function changes that support the changing ecology of the larva.

Most comprehensive studies of teleost development today are concerned with external aspects—morphometrics, meristics, pigmentation—for purposes of stage and species identification. Such information, though usually compiled for individual species (Watanabe, 1970; Louw and O'Toole, 1977; Doyle, 1977), also appears in massive regional surveys, such as the six volume "Development of fishes of the mid-Atlantic Bight" (Jones *et al.*, 1978). These data are crucial in fisheries, oceanographic, and environmental investigations, but usually contain only limited information on development of viscera and sensory organs. Other comprehensive studies of larvae are undertaken to compile baseline information for experimental work (Ballard, 1973), to extend knowledge of exotic life histories (Hulet, 1978) or to characterize development for taxonomic assemblages (Moser and Ahlstrom, 1970), and these often contain more information on internal aspects of development. However, there are also many studies undertaken to describe the development of particular organ systems in teleosts, usually to delineate the processes of differentiation involved, or to estimate functional and ecological parameters. In this paper I will review certain aspects of development in each of six organ systems, and their ecological implications, primarily as they occur in the northern anchovy, *Engraulis mordax*. Most of the information on the anchovy was derived from study of serial sections of specimens reared at 16–17°C in the laboratory of the Southwest Fisheries Center, La Jolla, California.

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TEMPERATURE AND GROWTH

Temperature can effect growth rate and hence the age-length relationship markedly in fish. The growth rate for northern anchovy reared at 22°C was about 1.75 times that of larvae reared at 17°C (Kramer and Zweifel, 1970), producing an average length of 13.3 mm at 17 days as compared to 9.5 mm at the lower temperature. Doyle (1977), in constructing a morphological staging system for *Clupea harengus*, estimated that time to metamorphosis was 153 days at sea temperatures (7–12°C) and 121 days at laboratory temperatures that were 1 to 3°C higher. Hayes *et al.* (1953) suggested that temperature or other factors could differentially effect the rate of development of different organs in *Salmo salar*, but Ballard (1973) found that such irregularities were generally minor.

In teleosts the variation in length for larvae of the same age usually increases with age. In anchovy larvae the coefficient of variation (SD/x · 100) was about 5% shortly after hatching, and increased to 15–20% by age 20 days (Kramer and Zweifel, 1970; Hunter, 1976). Whenever I examined such samples histologically, the extent of organ development varied with length rather than age.

Events in organ development of the anchovy are expressed in this paper in terms of standard length. The larvae I studied were reared at 16–17°C. At 16°C anchovy larvae hatch at 2.9 mm, reach 4 mm at three and a half days, 10 mm at 16.4 days, and 20 mm at 33 days (Hunter, 1976).

THE YOLK SAC PERIOD

At hatching the anchovy has a large yolk mass and pulsating heart, functional trunk musculature, lateral line neuromasts that are probably functional, and olfactory organs that may be functional. Most other organs are present as rudiments or appear and differentiate to a functional state by the time yolk is gone and feeding begins (4 mm). All systems increase greatly in complexity during the remainder of the relatively long larval period. Metamorphosis of the anchovy is considered to be complete by 35 mm SL when much of the body is scaled and digestive tract torsion is complete (Hunter, 1976). I will comment here on vitelline circulation, olfactory organs and Mauthner neurons before going on to descriptions of the integument, the lateral line system, the eye, the digestive tract, the gas bladder, and the trunk musculature.

According to Soin (1968) the vitelline or yolk sac circulation is developed poorly or not at all in Clupeiformes and many other pelagophilic teleost larvae because they do not need it as a specialized mechanism of respiration in oxygen rich waters. He implied that yolk absorption is accomplished by a different route. However, the entire yolk surface is a syncytial periblast which undoubtedly processes and delivers yolk to the circulatory fluid (Bachop and Schwartz, 1974). Al-Adhami and Kunz (1977) observed that while the only vessels on the yolk in *Brachydanio rerio* are the ducts of Cuvier, these fan out over the whole anterior part of the yolk sac so that blood cells are moving close to the yolk syncytium as well as the yolk sac ectoderm. In the anchovy the ducts of Cuvier are obvious over the front of the yolk mass and a subintestinal vitelline vein does attenuate rostrad on the posterior ventral surface of the yolk. My impression is that there is a diffuse movement of plasma over the yolk syncytium into the ducts of Cuvier. Capillaries are probably absent because the blood does not contain cells that need to be channeled. Though occasionally noticed in small numbers by day 7 or 8, erythrocytes were not consistently present until about day 14 or 15 when the larvae were approaching 10 mm SL.

The two olfactory primordia are small antero-ventral-facing ectodermal plaques between the eyes and the forebrain when the anchovy hatches. Each has a 20 μm depression on the free surface where the cells have a sensory epithelial organization (distal portions slenderized and nuclei located basally). Moreover, there are indications of cilia on the pit surface and a

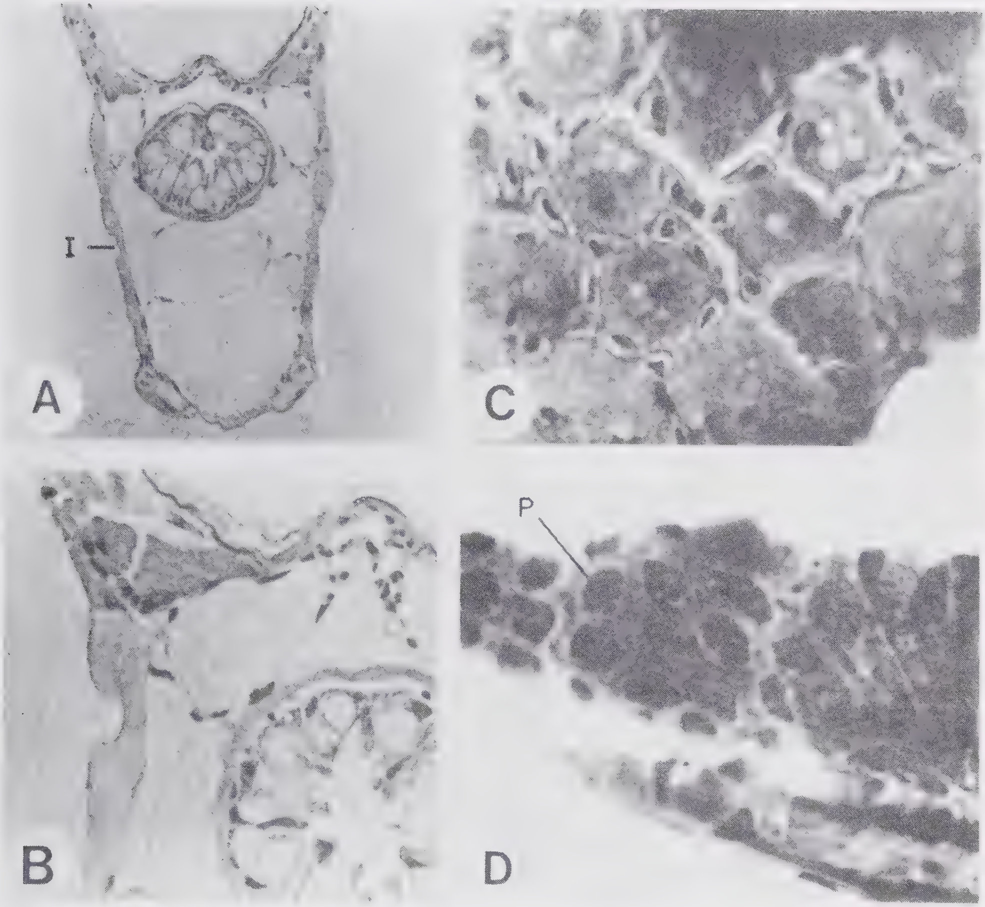

FIG. 1. Transient features of the epidermis of the anchovy larva. A. Cross-section of a 7 mm larva at the level of the esophagus. The lateral walls of the coelom are composed of large "chloride cells." One cell shows a central pit (I) indicating secretion to the exterior. ×100. B. Closer view of another cell with an excretory pit. ×630. C. Tangential section of the body cavity wall of a 14 mm larva. The chloride cells contain large vesicles, and the Malpighian cells surrounding the chloride cells are starting to proliferate. ×630. D. Sagittal view of the body surface of an 8 mm larva showing integumentary plate cells (P) that overlie the trunk musculature. ×400.

neuropil bridge extends from the olfactory capsule to the forebrain. In the cutthroat trout (*Salmo clarki*), which hatches at 35 days post fertilization, some axons extend from the olfactory epithelium to the brain at 20 days and recognizable cilia occur at 27 days, but cilia are not abundant until 40 days post-fertilization, or 5 days after hatching (Jahn, 1972). Jahn (1972) concluded that the cutthroat trout was probably capable of recognizing olfactory stimuli shortly after hatching. Though the anchovy has a much shorter incubation and yolk sac period, the probable existence of some cilia and the connection to the brain suggest that the olfactory system may function shortly after hatching. By 4 mm SL, when feeding begins, the olfactory plaques have shifted to a more dorsal position and enlarged slightly with some rostrad elongation.

I first found Mauthner neurons in anchovy larvae about 1 day after hatching. Kimmel (1972) observed that Mauthner

TABLE 1. *Summary of the development of the integument of the northern anchovy.**

Standard length (mm)	Observation
3.5	Epithelial plate cells differentiate Epithelial chloride cells differentiate
9.0	Epidermis starts thickening
10	Chloride cells start separating Dermis developing on head
17	Epithelial plate cells sloughed Goblet cells appearing
21	Chloride cells widely scattered
28	Scale development starts

* See text for details.

neurons (which mediate the startle response) are sometimes visible after 1 day of development in fish larvae. He concluded that the system is probably not functional until the fourth day of development because there is no well defined startle response over the next few days while the axons are extending towards the caudal region. Kimmel *et al.* (1978) showed that in the zebra fish the Mauthner cell "birthday," probably the earliest neuron birthday in the hindbrain, occurred during the late gastrula stage. Gideiri (1966) found Mauthner fibers extending to the tail at 56% of embryonic (pre-hatching) life in several species with long incubation periods.

INTEGUMENT

The development of the integument in the northern anchovy (Table 1) conforms in general with that of the plaice, *Pleuronectes platessa* L. (Roberts *et al.*, 1973) and with that of teleosts as a group (Bullock and Roberts, 1975). In newly hatched larvae the epithelial epidermis is two cells thick and subtended by gel-filled dermal spaces (including finfold spaces) over much of the trunk region. In the plaice there are some large "chloride cells" and a few mucous cells at this stage.

In the anchovy chloride cells are not found at hatching but are present by 3.5 mm SL. As yolk recedes, chloride cells differentiate over much of the wall of the pericardio-coelomic cavity (Fig. 1A). Occasional cells show a central pit, indicative of secretion to the exterior (Fig. 1B). Though the chloride cells are broad and contiguous, small Malpighian cells are present in the interstices among them from an early period. Beyond 10 mm SL the Malpighian cells start to proliferate (Fig. 1C) and the chloride cells gradually separate. By 20 mm SL the chloride cells are widely scattered and perhaps degenerating. The epidermis is thickening over the entire body at this time. The dermis starts to thicken in the head region at 11 or 12 mm SL, but remains thin on the trunk.

In many specimens the chloride cells contained a central cluster of clear vesicles (Fig. 1C). These may bear some relation to the surface pits observed in other specimens. Chloride cells in the skin of the larval puffer (*Fugus niphobles*) were often found to contain vacuoles filled with an amorphous substance that was released at the free apical surface of the cells (Iwai, 1969*a*).

Though chloride cells were not found in the herring (*Clupea harengus*) (Jones *et al.*, 1966), they were found in the Pacific sardine (*Sardinops caerulea*) (Lasker and Threadgold, 1968), where ultrastructural changes under osmotic stress and other factors indicated that these cells mediated osmoregulation in the developmental period preceding gill differentiation. Roberts *et al.* (1973) cautioned that it was not yet clear if integumentary cells of this kind found in the plaice and the sardine performed the same task as chloride cells found in the gills of mature stages of many fish. However, Bullock and Roberts (1975), in a review of the development of teleost skin, noted that for both species salinity stress did change the chloride cell volume without affecting the ordinary Malpighian cells.

Another transient feature of the epidermis of the anchovy larva is the presence of dense hyaline plates in the bases of the outer layer of cells. Such structures were reported in the Pacific sardine (Lasker and Threadgold, 1968) and the herring (Jones *et al.*, 1966). In the herring they were found in regions of the head, the buccal cavity, the yolk sac and the tail, and were believed to be either support structures or barriers to diffusion. In the anchovy all outer layer cells of the epithelium contain these plates over the trunk musculature (Fig. 1D). The plates are eosinophilic, and are detectable though not prominent one day after hatching. They grow rapidly and soon occupy most of the basal area of the cell. The plate cells extend onto part of the head and on the trunk they extend down to the junction with the wall of the pericardio-coelomic cavity. They overlap the upper margin of the chloride cell tissue only slightly. They extend onto the bases of the median finfold, but are entirely lacking over most of the finfold, where the nucleus is the only prominent structure within the epithelial cells. The plates on the bases of the finfolds soon move down against the musculature, as the muscle mass enlarges and the finfold narrows. These plate cells remain unchanged in appearance, except for enlargement, until the larva is 16 or 17 mm SL. By this time the epithelium has increased to five or six squamous layers and has shed the outermost cell layer containing the plates. The structural evidence in the anchovy—presence over the musculature, absence over the chloride cell tissue, and eventual disappearance when development of functional gills and a thickened integument are well along—indicates that the plates constitute a diffusion and an osmotic barrier.

THE LATERAL LINE SYSTEM

Most teleosts hatch with a series of latero-sensory neuromasts on the head and trunk that are functional or very close to being functional. The goby (*Tridentiger trigonocephalus*) has three pairs on the head and five on the trunk, all with gelatinous cupolae, when it hatches at 2.6 mm on day 7 (Iwai, 1963). The Japanese medaka (*Oryzias latipes*) has 8 pairs of neuromasts with cupolae just starting to bud at hatching, but the cupolae are well developed 20 hr later (Iwai, 1964). The newly hatched pilchard (*Sardina pilchardus*) has neuromasts with prominent cupolae at least on the trunk (Blaxter, 1969). Meyer-Rochow (1972) did not find cupolae on neuromasts of larvae of *Cataetyx memorabilis* but concluded that this was an artifact of fixation and that the organs probably were functional because they were innervated. Cahn *et al.* (1968), using silver staining techniques, concluded that neuromasts of *Menidia* were not innervated until the larvae, which hatch at 4 mm, were 7 mm in length and tentative schooling activity was starting.

At hatching the anchovy has one row of neuromasts along each side of the trunk and three or four pairs on the head, and all have cupolae (Fig. 2). Each row of trunk neuromasts is closely subtended by a lateralis nerve that extends back between the musculature and the epidermis from the posterior tip of the post-otic vagus ganglion (Fig. 3). A slender nerve root from the anterior tip of the ganglion penetrates the floor of the hindbrain. There is also a pre-otic ganglion on each side, and presumably these provide innervation for the head neuromasts.

After hatching, the neuromasts on the head increase in number and in diameter more or less in proportion to standard length. At 33 mm SL there are almost 50 pairs of organs on the head, and they are about 150 μm in diameter, as compared to 25 μm at hatching. Canal formation starts with development of a lateral recess in the temporal region at 18–20 mm SL, as in the herring (Allen *et al.*, 1976). The various branches gradually extend over the head from the recess, enclosing the developing neuromasts. During and following the last stages of canal formation, a new set of neuromasts, small surface pit organs, differentiates on the head. At 33 mm SL there are more than 80 pit organs on each side; they are not much larger than the original neuromasts were on the newly hatched larva.

The neuromasts on the trunk also increase in number as the anchovy larva grows. By 20 mm SL there is a dorsal and a ventral line of organs in addition to the midline. As growth continues these become patches of perhaps as many as four pit organs at each location. In juveniles the pit organs are always located over exposed portions of scales.

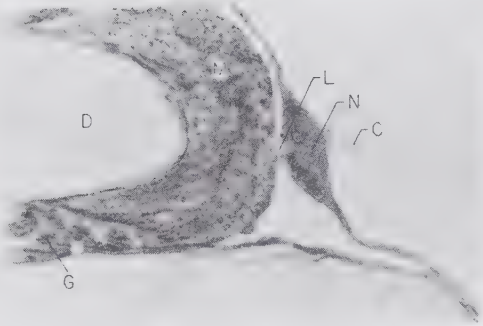

FIG. 2. Cross-section of a newly hatched anchovy larva showing a trunk neuromast (N) with a gelatinous cupola (C) and underlying lateralis nerve (L). The trunk musculature (M), notochord (D) and rudimentary foregut (G) are also visible. ×630.

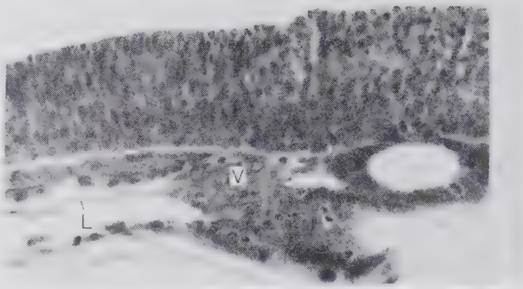

FIG. 3. Sagittal view of the vagus ganglion (V) and lateralis nerve (L) of a newly hatched anchovy larva. The ganglion is behind the otic capsule and below the hindbrain. ×400.

In the Cyprinidae and some other teleosts the neuromasts appearing in the larval and juvenile stages are known to arise differently than the primary neuromasts present at hatching. Disler (1960) observed that the primary neuromasts in the Cyprinidae develop in the embryo from subcutaneous primordia related to the preauditory and postauditory ganglion plaques, whereas the later appearing neuromasts arise *in situ* from the basal layer of the epidermis under the influence of nerve endings. In regard to function, he postulated that the organs enclosed in canals were thus shielded from small local disturbances, which would then only be registered by the surface neuromasts.

THE EYE

Differentiation of the retina will be described elsewhere in this symposium, so I will make just a few observations about the anchovy eye, which are summarized in Table 2.

TABLE 2. *Summary of the development of the eye of the northern anchovy.*

Standard length (mm)	Observation
3.5	Oculomotor muscles differentiated
4.0	Photopic visual system functional
5.0	Area temporalis present
7.0	Lens retractor muscle appears
10.0	Earliest incidence of rod differentiation

The retina of the anchovy is undoubtedly functional when feeding starts at about 4 mm SL. The visual cells are more slender and abundant towards the temporal part of the eye. By 5 mm SL there is a point of maximum visual cell density not far from the ventro-posterior margin of the retina and perhaps 20° below the horizontal meridian, constituting an *area temporalis*. The center point of the *area* is identifiable from the lateral view (Fig. 4) because nuclei of the outer nuclear layer tend to be laterally displaced and slanted towards this point, probably to accommodate the close packing of the slender visual elements. The surface of the eyeball is also slightly peaked at this point, probably to accommodate increased length of the visual elements.

The lens retractor muscle does not appear until 7 mm SL, after which it increases steadily in size. The six oculomotor muscles, on the other hand, are well differentiated with typical teleost insertions around the periphery of the eye by 3.5 mm SL, when feeding activity should be starting. Considering these features, it is reasonable to assume that the early feeding anchovy larva has a well defined axis of maximum visual acuity, and good eye mobility, and therefore can probably exercise an effective binocular vision in aligning itself to close objects. There is probably some depth of focus at the start, and the ability to accommodate to greater distances must increase as the retractor muscle

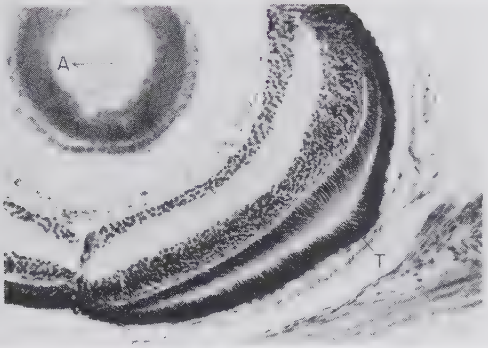

FIG. 4. Sagittal view of the *area temporalis* (T) of the left eye of an 11.6 mm anchovy larva. (A) indicates the anterior direction. ×250.

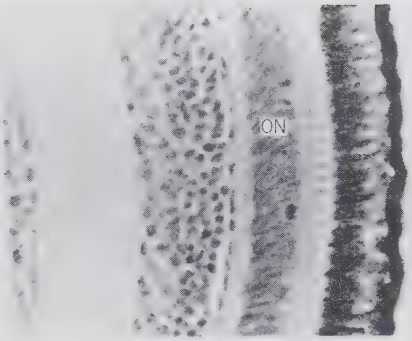

FIG. 5. Cross-section of the retina of a 16 mm anchovy larva with two mitotic figures in the outer nuclear layer (ON). ×630.

grows after 7 mm; this would increase the perceptive field for feeding.

Although the adult anchovy has a well developed duplex retina with abundant rods as well as cones (O'Connell, 1963), the early larva appears to have a simplex retina in which the one class of visual cell is presumed to be cones. The outer nuclear layer does become 2-tiered as the visual elements are first budding, and this could signify early appearance of rods along with cones, but since the broadly overlapping nuclei of the two tiers have the same elongate appearance, it is more likely that they indicate the differentiation or formation of twin cones. Grün (1975) described a double layer of nuclei in the outer nuclear layer of the early stage retina of *Tilapia leucosticta* and identified both rods and cones in electron micrographs of initial visual cell differentiation. In this case, however, the nuclei of each of the two layers were different in character. Functioning rods were not found in the retina of *Nannocara anomala,* another cichlid, until day 16, although free swimming (and vision) starts on day 5 (Wagner, 1974). Rods were first found at 20 mm in the retina of the herring, *Clupea harengus* (Blaxter and Jones, 1967). In the anchovy the outer nuclear layer remains 2-tiered until 10 or 12 mm SL, after which mitotic figures are occasionally found and the layer increases to three and soon to four and more tiers of nuclei, undoubtedly indicating rod recruitment, which is well underway when the larvae are 16 mm in length (Fig. 5).

Thus, while variations in timing exist, rods probably appear sometime later than cones in many teleosts. In the anchovy a continual recruitment of rods occurs for a long period, and there is probably a commensurate increase in visual sensitivity. Such a developmental sequence appears to be adaptive to the changing feeding and behavioral patterns described by Hunter (1972) for the anchovy. When rods start to appear after 10 mm SL, vertical migration is also starting (Hunter and Sanchez, 1976), and larvae are moving into and becoming more active in dimmer light.

THE DIGESTIVE TRACT

As is the case with many marine teleosts, the northern anchovy hatches with a large yolk mass, no mouth, and a rudimentary gut. The gut differentiates to a functional digestive tract by the time yolk is exhausted in a few days, but there is extensive development beyond this point, as outlined in Table 3. While there is no mouth at hatching, there is a spiracle-like opening extending laterally under each otic capsule from the rudimentary pharynx (Fig. 6). This is the hyobranchial cleft, separating the presumptive mandibular and hyoid arches from the presumptive branchial arches. By the time yolk is exhausted the mouth and a simple hyoid suspension have differentiated. The lower jaw has grown to

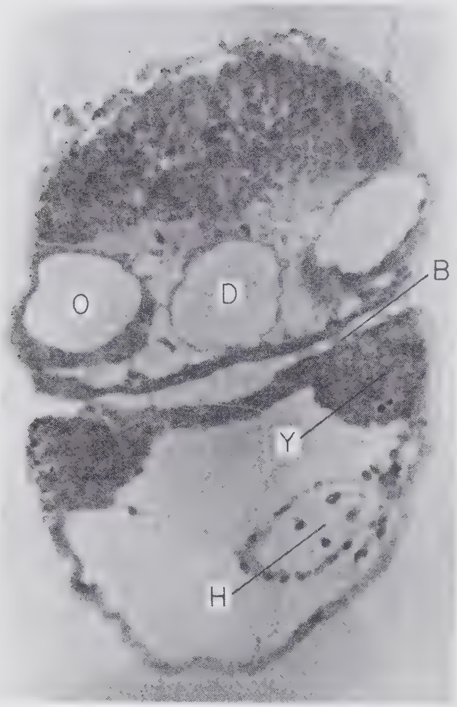

FIG. 6. Cross-section of a recently hatched anchovy larva at the level of the otic vesicles (O) and heart (H) to show the spiracle-like hyobranchial clefts (B) that extend lateral from the rudimentary pharynx at time of hatching. (Y) is an element of the developing hyoid arch and (D) is the notochord. ×250.

almost the length of the snout and there is a jaw joint (mouth corner) where the mandibular cartilage articulates with the hyomandibular above. The hyoid cartilage, still a bar behind the mandible, articulates with a small caudad extension of the hyomandibular. Flüchter (1962) described the junction of the mandible with the hyomandibular in first feeding herring as a narrow, flexible continuation rather than an articulation. The branchial apparatus is also well formed in the anchovy when yolk is exhausted, with three gill clefts open. There are also two upper and two lower tooth capsules at the back of the pharynx, which become functional recurved teeth as feeding starts and undoubtedly guard against reverse movement of material from the esophagus into the buccal cavity.

TABLE 3. *Summary of the development of the digestive tract of the northern anchovy.*

Standard length (mm)	Observation
3.0	No mouth; gut rudimentary
3.5	Liver, pancreas differentiated
4.0	Mouth and digestive tract functional
4.5	Four pharyngeal teeth present
15	Upper limbs of branchial arches start differentiating
19	Eight pharyngeal teeth present
20	Upper limbs of branchial arches becoming free
21	Gastric glands, pyloric caecae start differentiating
22	Jaws lengthening
24	Stomach blindsac buds

They increase in number during larval growth.

When feeding starts, the digestive tract proper is composed of a foregut, midgut and hindgut. In the anchovy the foregut is relatively long with the liver and compact pancreas beneath the rear portion. The digestive tract remains straight during the larval period, except for a vertical flexure and constriction denoting the pyloric valve. The midgut is larger in diameter than the foregut. The gas bladder diverticulum appears at top left of the flexed region perhaps two days after hatching. In the larvae of many fishes, such as the Pacific mackerel (*Scomber japonicus*), the anus is much further forward on the body and the foregut is short, but a strong lateral flexure and expansion occurs in the pyloric region as feeding begins.

The midgut mucosa in the anchovy is composed of absorptive cells that are cuboidal or low columnar at best. Ridges are incipient and they develop during the larval period by mitosis of the mucosa cells, which in the anchovy seems to occur late at night when the digestive tract is empty. Mitosis of mucosa cells has been found to occur in certain spatial patterns in the sea lamprey (Youson and Connelly, 1978), and also in *Xenopus* (Marshall and Dixon, 1978). In the anchovy the midgut ridges are transverse, and give the midgut a vertical striated appearance in later larvae. Louw and O'Toole (1977), in the course of describing larval development of *Sardinops ocellata,* comment that this feature is probably responsible for some earlier workers regarding the posterior gut as convoluted.

The hindgut is not easily distinguished from the midgut until feeding starts, at which time each mucosa cell in the hindgut develops a large supra-nuclear eosinophilic inclusion body that appears to have an intimate relation with the nucleus (Fig. 7). Such bodies occur also in the Pacific mackerel and have been reported for other fish larvae, but there is still uncertainty about their role in the digestive process. Iwai (1968, 1969*b*) and Iwai and Tanaka (1968) found such structures in the hindguts of certain freshwater teleosts and suggested that they were indicative of intracellular digestion of proteinaceous food particles engulfed by pinocytosis. It is not known whether pinocytosis occurs in the anchovy, or whether the bodies are proteinaceous. Govoni (1980) found similar bodies in the hindguts of larval *Leiostomus xanthurus,* but questioned their presumed role as a pregastric protein digestive mechanism because they continued to be present after complete stomach differentiation. Gauthier and Landis (1972) considered the role of such structures found in adult *Carassius auratus* to be intracellular (protein) digestion.

In the anchovy major changes in the digestive tract (considered part of metamorphosis) start at about 20 mm SL. Gastric pits appear behind the pneumatic duct origin, the pyloric flexure strengthens and shows a few pyloric caecal buds. Within a few days, as the fish approaches perhaps 24 mm, the stomach blindsac buds from the dorsal wall of the pylorus, and the pylorus begins to bulge forward below to form the cardiac portion of the stomach. Late differentiation of the stomach is common in teleosts, and implies a shift towards ingestion of larger quantities of food in short periods (Reifel and Travill, 1978), and perhaps a shift to a diet heavier in protein. In the plaice, the stomach starts to differentiate at 20 days and peptidic activity increases sharply at about 30 days (Yasunaga, 1972). In *Plecoglossus,* gastric glands start to develop at about 25 mm and pepsin-like activity rises from virtually none to a much higher level by 40 mm than amylase or trypsin activity (Tanaka *et al.,* 1972). Bream (*Acanthopagrus*) has a pattern of digestive enzyme development similar to that of *Plecoglossus,* while the carp (*Cyprinus*) develops trypsin and amylase activity gradually from hatching but shows only insignificant pepsin activity (Kawai and Ikeda, 1973). Bream shifts from smaller zooplankton to larger zooplankton and fish at metamorphosis, while the carp is stomachless as an adult.

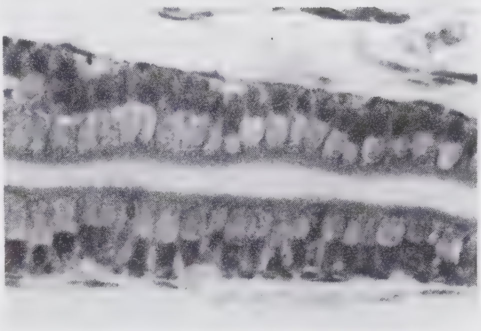
Fig. 7. Sagittal view of the hindgut of a 5.6 mm anchovy larva. The large eosinophilic inclusion bodies are in close contact with the basal nuclei. ×630.

In anchovy larvae of about 15 mm changes start in the jaws and branchial apparatus that indicate a change in feeding mode. As Flüchter (1962) noted for the herring larva, the gill arches are almost straight and extend obliquely up and back in the early feeding anchovy. Arches I through IV are composed of small basibranchials and hypobranchials, and long ceratobranchials, which terminate in dense connective tissue below the otic vesicle (Fig. 8). This arrangement means that mouth opening is essentially a lower jaw movement. At about 15 mm SL the upper limbs of the branchial arches begin to condense in the tissue of the palate and they begin to break free by 20 mm. The upper limbs remain relatively short until about 23 mm, when they are clearly differentiated into epibranchials and pharyngiobranchials with some development of rakers and gill septa (both of which had started much earlier on the lower limbs). At this time the

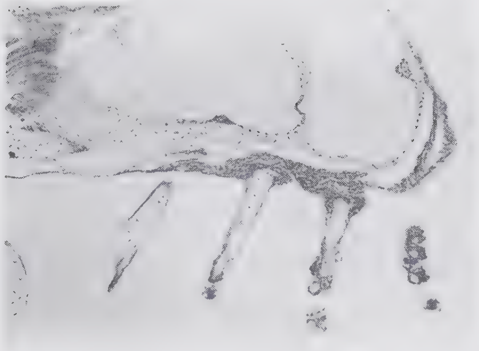

FIG. 8. Sagittal view of branchial arches II and III on left side of an 11.6 mm anchovy. The upper ends of the ceratobranchials join dense connective tissue of the palate below the developing ear. Upper limbs of the arches have not yet differentiated. Some parts of gill filaments with lamellae are visible. ×100.

branchial arches start to lengthen, as do elements of the snout and the upper and lower jaws. This sequence of events (and some changes in the suspensorium) results in a mouth of large and expandable gape involving mobility of upper and lower jaws and branchial elements. It is probably becoming functional as a filter feeding apparatus before the larva reaches 30 mm SL.

THE GAS BLADDER

The gas bladder, an organ unique to teleosts, is one of the few systems that is not present when the anchovy larva starts to feed. It is represented at this time by a bulge in the dorsal wall of the pyloric flexure; it splits the ridge of primordial germ cells as it rises. Within a few days it is a small thick-walled rudiment with a patent lumen and a short pneumatic duct originating from the upper left surface of the pyloric flexure. The clupeoids are the only large group of ocean fishes that have pneumatic ducts as adults (Marshall, 1966), and they are also the only group with a rostral extension of the gas bladder that is in intimate contact with the inner ear. In the anchovy this extension first appears at about 5 mm SL as a slender tubule with a slightly bulbous tip that grows forward from the anterior tip of the rudimentary bladder. It bifurcates when beyond the pectoral girdle and reaches the prootic cartilage at 9 or 10 mm SL. The development of the gas bladder in the northern anchovy is outlined in Table 4.

TABLE 4. *Summary of the development of the gas bladder of the northern anchovy.*

Standard length (mm)	Observation
5	Bladder anlage appears
9	Anterior duct of bladder reaches ear
10	Bladder inflates Musculature of bladder wall starts differentiating
15	Bladder thin walled; highly contractile
28	Anterior bladder chamber differentiates

As the rostral extension approaches the prootic cartilage, the bladder itself has enlarged but is still less than half a millimeter long and smaller in diameter than the digestive tract. The lumen is a narrow horizontal slit and the wall is relatively thick, composed of a pavement epithelium of large cuboidal cells (continuous with the digestive tract mucosa) and a thick, dense layer of transversely aligned mesenchyme or myoblast cells (Fig. 9). This layer is continuous with a thin layer of splanchnic mesenchyme cells that invest the pneumatic duct and pyloric valve region. Both of these layers are part of what will be the tunica interna of the bladder. Schwarz (1971) described a similar layer of mesenchyme cells continuous with the mesenchyme layer of the gut in the bladder wall of the haddock embryo. In anchovy larvae of 10–12 mm the lumen often shows a degree of distension, but the wall does not expand or change in thickness. Beyond this size range the wall changes rapidly in character. The pavement epithelium is thinning and myoblasts become longer and more slender smooth muscle fibers. Bladder walls characterized by myoblasts are on the order of 20–25 μm thick. By 15 or 16 mm SL the musculature is well developed and the walls can be less than 10 μm thick when the bladder is expanded. As the anchovy is approaching 25 mm SL the bladder is about 5 mm long and somewhat larger in diameter than the digestive tract when fully inflated.

The growth in length of the bladder is exponential. That is, at 6 mm SL the bladder is 2% of standard length, at 16 mm it is 6%, and at 30 mm about 15%. At about 28 mm SL an anterior chamber develops from the posterior part of the slender rostral extension. This anterior chamber connects to the much larger posterior chamber through a thin sphincter, which must increase in complexity as well as size to achieve the configuration described for the adult (O'Connell, 1955). The cartilaginous sheath of the rostral extension differentiates as the anterior chamber differentiates.

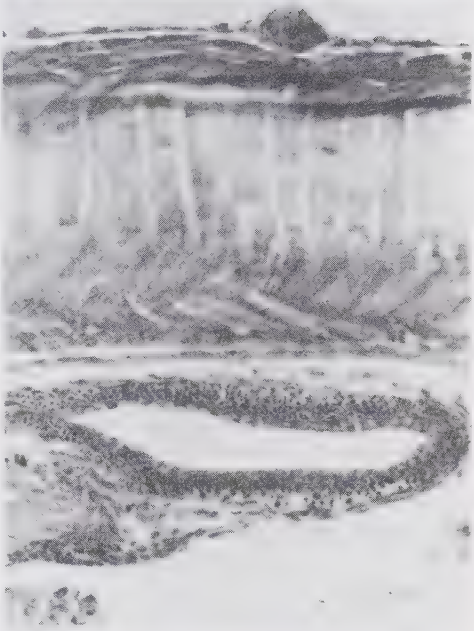

FIG. 9. Sagittal view of the gas bladder of an 8 mm anchovy larva. The bladder wall is still myoblastic but the lumen shows some expansion. The vertical structures above are developing collaginous bands of the notochordal sheath. One lateral line neuromast is visible. ×250.

One area of preoccupation with gas bladder development has been the mode and timing of initial inflation, which can have implications for energy conservation and survival *vis á vis* the ability to adjust buoyancy. The salmon and the brook trout probably inflate by gulping air at the surface, and initial inflation can be delayed several days by the presence of strong water currents that would sweep alevins off station (Saunders, 1964). Cichlids, which do not have pneumatic ducts even in the early stages, apparently inflate by internal gas secretion (McEwen, 1940; Doroshev and Cornacchia, 1979). The cichlid, *Tilapia mossambica,* and the striped bass, *Morone saxatilis,* which has a pneumatic duct and possibly inflates by surface gulping, both showed critical periods of time during development, after which normal inflation, if delayed, was impossible (Doroshev and Cornacchia, 1979). The larvae of several clupeoids, including *Engraulis mordax,* have been shown to undergo a daily cycle of bladder inflation and contraction in conjunction with vertical migration (Uotani, 1973; Hunter and Sanchez, 1976). The northern anchovy, *Engraulis mordax,* which starts this pattern at 10 mm SL, evidently cannot accomplish daily inflation without access to the surface, and it appears that inflation may be a mechanism to conserve energy during nighttime non-feeding hours (Hunter and Sanchez, 1976). The differentiation of the bladder musculature, described above, appears to take place in the anchovy during the first days that the bladder inflation-contraction cycle is operating.

Uncertainty about the function of the gas vesicles associated with the inner ear in clupeoids continues to generate investigation of this mechanism. While the question of function is usually addressed to the system as it exists in adults, Blaxter and his co-workers (Allen *et al.*, 1976; Blaxter and Denton, 1976; Denton and Blaxter, 1976) considered the function of the system in early as well as mature stages. They found that the prootic bulla (adjacent to the ear) first appeared at 18 mm SL in the herring, started filling with gas at 25 mm, and was always full by 30 mm. They considered that in the adult the gas bladder proper served as a reservoir to maintain gas at a constant volume in the prootic vesicle under changing ambient pressure. This

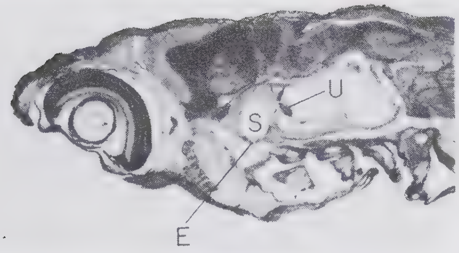

FIG. 10. Sagittal view of a 16 mm anchovy larva showing the gas vesicle (S) in the prootic bulla, which still includes areas of fibroelastic membrane (E). The branches of the macula utriculus (U) are distinguishable but not yet well separated. ×25.

would preclude distortion of an associated resonating membrane that presumably responds to and enhances transient vibrations that are transmitted to a portion of the inner ear. In larvae, before the bulla enclosing the vesicle was rigid, the membrane sustained appreciable distortion under ambient pressure changes, and could be part of a pressure sensing system (in the range 30–40 mm SL).

The system in the anchovy develops essentially as described for the herring. It should be noted, however, that the prootic vesicles tend to inflate at about 12 mm SL when the bladder itself first inflates, but great variation occurs. Some of this variation appears to be associated with the inflation-contraction status of the bladder up to about 25 mm SL. Up to this size the bulla enclosing the vesicle is composed of surfaces of the prootic and certain other cranial cartilages and fibroelastic membranes bridging gaps between them (Fig. 10). At this size intramembranous bone starts to develop in these membranes and also in the area where the edges of the fenestra will project toward the utriculus wall. By 30 mm SL all of these areas are solid bone, more distinctly so than any other elements in the head. Beyond this size, or probably beyond 25 mm SL, the vesicles appear to remain inflated all the time. The bladder may then function primarily as a reservoir to maintain the vesicles in the face of external pressure change as suggested by Allen *et al.* (1976), whereas it appears to function primarily as a buoyancy device in smaller larvae (Hunter and Sanchez, 1976).

One of the most recent observations on the function of the ear-gas bladder connection (Popper and Platt, 1979) indicates that the orientation pattern of hair cell bundles on the divided sensory macula of the utricle is unique among vertebrates and not incompatible with the argument that the (herring) utricle may respond to acoustic stimuli. An important feature of this mechanism is the division of the utricular maculus into three lateral branches or "fingers," with the fenestra of the prootic bulla facing the space between the anterior and medial branches. In regard to development, I have observed in the anchovy that the separation of the utricular maculus into three branches starts at about 12–14 mm SL and is not well defined until 18 or 20 mm SL. The size range over which the macular branches differentiate coincides generally with the range in which inflation of the prootic vesicle is highly variable.

TRUNK MUSCULATURE

The myotomes of fish contain two main types of muscle fibers: "fast" white fibers presumed to be important in burst activity, and "slow" red fibers presumed to be important in slower cruising activity. According to Bone (1978) there is considerable uncertainty about how these two types differentiate and how the two populations change in proportion during growth. In general, it appears that differentiation proceeds from the inner myotome face outward, with deep myoblasts differentiating into white fibers and surface myoblasts later differentiating into superficial red fibers (Waterman, 1969; Nag and Nursall, 1972). Red fibers are generally smaller than white fibers as well as superficial, but small fibers have been found among the white fibers in later developmental phases of several species; in clupeids and gadoids the small fibers appear to be growth stages of the white fibers, but for salmonids it is not yet clear whether they are "slow" fibers or simply growth stages of "fast" white fibers (Bone, 1978).

Development of the musculature of the northern anchovy, which is outlined in Table 5, exhibits some of the variable features mentioned above, but in addition it shows a specialized organization at hatching. There are two layers of fibers aligned obliquely in opposite directions, and interdigitating to form a kind of basketweave configuration (Fig. 11A). These fibers each have a number of axial nuclei and a thin peripheral layer of myofibrils. Presumably they had arisen by fusion of mononucleate myoblasts prior to hatching. This musculature, which is myotomal but thin relative to the large notochord, is probably characteristic of at least the clupeoids. It is obvious, for instance, in newly hatched *Sardina pilchardus* (Blaxter, 1969). By contrast, *Scomber japonicus* has relatively thick musculature at hatching and fibers have a near-horizontal alignment. In the anchovy the oblique fibers, which enlarge as the larva grows, are prominent to about 20 mm SL. They could not be identified in larvae approaching 30 mm, but might still be present against the notochord.

TABLE 5. *Summary of the development of the trunk musculature of the northern anchovy.*

Standard length (mm)	Observation
3	Embryonic oblique muscle fibers only
4	Myotube generation of white fibers starts
6	White fiber mass thickening dorsally and ventrally. Red fibers appear, single superficial layer
10	White fiber mass covers midline of body
12	White fiber mass well above spinal cord
16	Red fibers 2–3 layers thick at midline
20	Red fibers 3–4 layers thick at midline
21	Myosatellite cell proliferation of white fibers starts
23	Myotube generation of white fibers declines
26	Red fibers 7–8 layers deep

The addition of new muscle fibers over the surface of the oblique musculature starts at 3.5–4.0 mm SL. The fascia on the outer surface of the myotomes produces a compact matrix of very small myotubes that contain just a few slender myofibrils. Proliferation starts dorsally and ventrally, filling in against the spinal cord and dermatome as it also extends toward the midline. The fibers enlarge steadily as they are overlaid by new surface additions (Fig. 11B). The myofibrils within them are laminar and radially disposed, and undoubtedly increase in size and number by branching, splitting, and addition of myofilaments centrifugally, as described by Patterson and Goldspink (1976). This myotube musculature finally covers the oblique musculature at the midline at about 12 mm SL. By 20 mm it is moderately thick at the midline and has risen well above the spinal cord dorsally as already indicated; these fibers have a near-horizontal alignment. Surface addition by myotube proliferation declines appreciably beyond 20 mm SL, remaining highest, perhaps, near the lower margin of the muscle mass, which is in the process of extending ventrally in the wall of the body cavity.

As surface addition declines, small muscle fibers appear among the larger ones, noticeable first in the deeper portion of the myotomes. Eventually they are abundant and widespread, and of various diameters (Fig. 11C). They must arise from the large fibers by myosatellite cell differentiation, as has been suggested by others (Greene and Greene, 1913; Bone, 1978; Greer-Walker and Emerson, 1978). All of the above constitute the white muscle mass of the trunk.

The red musculature first arises in the anchovy not long after the myotube addition of white muscle fibers has started. It appears at 6 or 7 mm as a single layer of fibers on the outer face of the myotube-producing membrane. The fibers are aligned horizontally and have the more or less rectangular cross section characteristic of the type in the anchovy (Fig. 11B). They also characteristically have a high myoplasm content with one or two serpentine arrays of well spaced myofibrils. Loose packing of myofibrils and high myoplasm content was noted for red or superficial fibers of the zebra fish (Waterman, 1969) and the cod (Greer-Walker, 1970). The same arrangement occurs in the sound

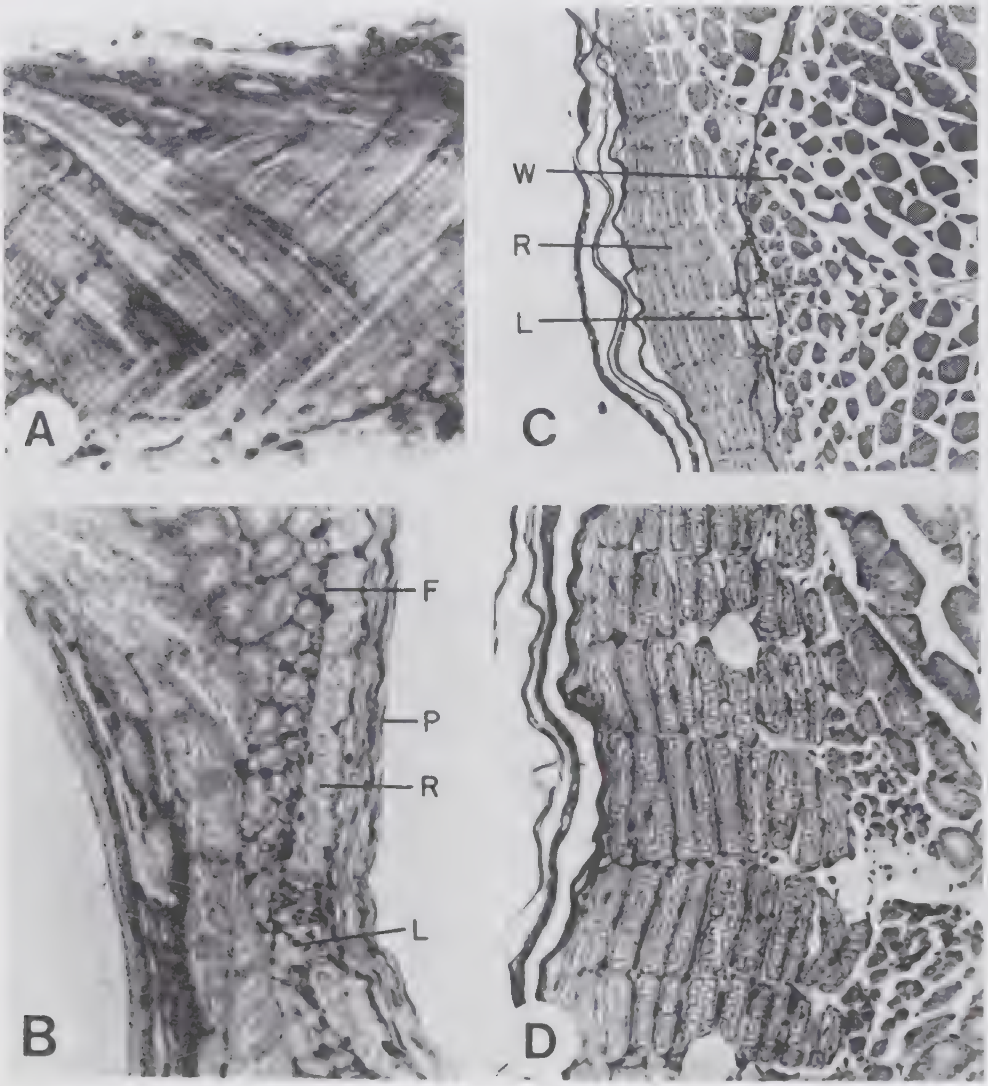

FIG. 11. The trunk musculature of the anchovy larva. A. Sagittal, tangential section of a 7 mm larva showing the oblique muscle layers that are dominant in the early weeks. ×100. B. Cross-section of the trunk musculature of a 14 mm anchovy above the midline. The large fibers close to the notochord are the original oblique fibers. White fibers are added by myotube differentiation at the fascia (F) and increase in diameter as more new fibers are added at the surface. The light band outside the fascia is a single layer of red fibers (R) above and below the lateralis nerve (L). The epidermis has about four layers of squamous cells, the outer layer containing hyaline plates (P) ×400. C. Cross-section of a 33 mm larva, showing many smaller white fibers (W) that arise by satellite cell differentiation from the larger fibers. The zone of red fibers (R) laterad of the lateralis nerve (L) is multilayered. ×25. D. Cross-section of the red muscle zone of a 31 mm larva. Close pairing of some fibers indicates that red fibers proliferate by equal division. ×250.

muscle of the cod, where it is presumed to promote a high rate of metabolism and fast twitch activity (Odense *et al.,* 1978).

The red muscle tissue remains a single layer of growing fibers interrupted only by the lateralis nerve at the midline until the anchovy reaches a length of about 14 mm, when a second layer may appear, and when a small zone of small nondescript fibers becomes evident around the lateralis nerve. This is the intermediate zone as described by many workers, and it is the only group that cannot readily be classified as either the white or the red type. When a third layer of red fibers appears at 18–21 mm SL, one or two of the red fiber layers usually cover the lateralis nerve. By 30 mm there are 8–10 layers outside the lateralis nerve, and the typical triangular cross section of the midline band of red muscle is evident.

The manner of red fiber proliferation is not clear. The first layer quickly covers the surface of the myotome when it appears and possibly is produced by myotube generation from the outer face of the fascia covering the myotome. Additional layers may arise in this way, but the "intermediate" fibers around the lateralis nerve may also be involved. However, frequent close pairing among the red fibers indicates that they may proliferate by equal vertical division (Fig. 11D).

The different phases of muscle development are distinct and occur in sequence, although with broad overlap. Presumably each phase has some adaptive role in the growth and changing behavior of the fish. The oblique musculature that is dominant for the first few weeks possibly confers some advantage relating to the elongate body form and the sustained S-shaped posture that precedes food strikes (Hunter, 1972). The second phase of muscle development, myotube generation at the surface, probably serves in the anchovy to gradually superimpose the fusiform body shape of the juvenile on the elongate body shape of the larva. The myosatellite phase, on the other hand, probably serves to further enlarge the muscle mass without appreciably altering body or myomere form. The superficial red musculature, though it originates early, does not show any appreciable thickening until the myotube addition of white musculature has almost run its course at 20 mm SL. Schooling behavior is in a formative stage at 20 mm, and continues to develop as the fish grows beyond this (van Olst and Hunter, 1970).

CONCLUDING REMARKS: ANCHOVY AND MACKEREL

The features of development described here demonstrate that in the anchovy most organ systems are functional after only a brief, early rudimentary period, and then increase in complexity and size throughout the larval period, expanding functional capabilities and ecological interaction together. This sometimes includes appearance and disappearance of transient structures, but more often relates to the differentiation and gradual recruitment of new elements in a system. Behavior patterns, in fact, tend to change gradually in close conjunction with these recruitment processes. Such a relationship may apply widely to teleosts, but at the same time the pattern and tempo of development among species may differ considerably from that of the anchovy, even where the larvae similarly hatch from pelagic eggs after a short incubation period. One of the more obvious contrasts is that of mackerel and anchovy.

Hunter (1981) states that while adults of different marine species may feed in various specialized ways, the larvae are all diurnal particulate planktivores with feeding behavior that is most similar at first feeding, but diverges as development proceeds towards metamorphosis. He frequently contrasts the northern anchovy, *Engraulis mordax,* and the Pacific mackerel, *Scomber japonicus,* as representatives of the "sinuous" clupeoid type and the more rigid, more agile scombroid type. Larvae of the anchovy strike only once at food items from a carefully adjusted S-shaped posture. Larvae of the mackerel feed "in a manner more typical of the biting attack of many adult fishes" and frequently repeat if the strike misses. Body depth and head size, and also mouth size and thus

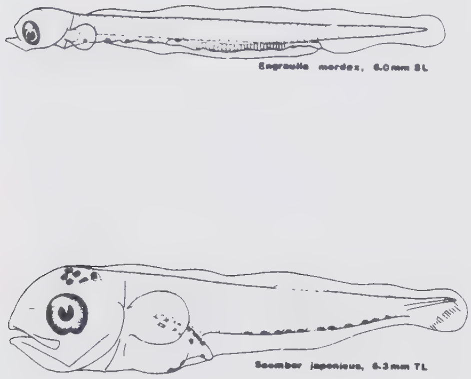

FIG. 12. The northern anchovy and the Pacific mackerel (after Watanabe, 1970) at about the same length. Both species would be expected to reach these lengths about 9 or 10 days after hatching at 16–17°C.

prey size increase more rapidly in the mackerel than in the anchovy. The mackerel becomes piscivorous at 10 mm SL.

The anchovy and the mackerel hatch at about the same length but with different body configurations, and within a few days they differ strikingly in body form (Fig. 12). The anchovy has an almost anguillid form with a long digestive tract, and thus it has a long trunk and a short (post-anal) tail. The mackerel has a short visceral mass in which organs tend to be spheroid and flexures appear early. According to Watanabe (1970) torsion of the gut occurs during the yolk sac stage and the stomach is formed at 10 mm. Consequently the trunk is short and the post-anal tail is long. In contrast to the thin oblique musculature of the anchovy, the first-feeding mackerel has relatively thick musculature with fibers in a near-horizontal alignment that foreshadows the definitive adult arrangement (though without red muscle development). Fibers grade from small to larger diameter mesially, which suggests that new additions occur over the entire surface of the myomere essentially from hatching. This would permit uninhibited increase in body depth, and along with it head depth.

The mackerel, of course, is a particulate, piscivorous feeder as an adult, and this is quite close to the feeding mode that is obligate for all larvae in the plankton. The anchovy, on the other hand, is primarily a filter feeder as an adult, and this is quite different than the obligate larval mode. The difference in the early and later feeding modes of this species is probably responsible for the notable metamorphosis it undergoes, which includes marked changes in the locomotor apparatus, the digestive tract and the jaw-branchial apparatus. In the mackerel, since feeding mode does not change in kind, development can progress towards the definitive adult configuration from an early stage. For example, the mackerel shows branchial arches with free, albeit short, upper limbs by 10 mm SL. The mouth and branchial apparatus can enlarge without restriction during early growth, whereas in the anchovy changes in jaws, branchial arches and suspensorium towards the wide gape capability of the filter feeding mode would probably be unwieldy in the particulate feeding larval period. The mouth of the anchovy larva is relatively small, possibly because of these developmental limitations, and this in turn may account in part for the precise nature of the feeding attack.

Between them, the northern anchovy and the Pacific mackerel probably represent the developmental patterns of a large portion of larvae that occur in the marine plankton. There are several dozen genera of Clupeoidei, most of which are filter feeding planktivores, and there are over a dozen genera of Scombridae (and probably several genera of Carangidae), all of which are pelagic marine carnivores. However, the plankton supports larvae of many other teleosts, the adults of which may be adapted to different ecological niches than either of the above. Thus, clupeoids and scombroids aside, there are probably many other patterns of development, resulting from accommodation to different adaptations of the adult along with the universal necessities of the larval period in the plankton.

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ESTIMATION BY HISTOLOGICAL METHODS OF THE PERCENT OF STARVING LARVAE OF THE NORTHERN ANCHOVY (*ENGRAULIS MORDAX*) IN THE SEA

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One of the goals of pelagic fish stock investigations is to predict how large year-classes will be at the time of recruitment to the adult population. While the primary approach to this problem for the northern anchovy (*Engraulis mordax*) is the estimation of larval mortality rates on the basis of abundance estimates from egg and larval surveys, other methods are being sought for corroborative purposes, or to reduce time and costs. The approach described in this report is estimation by histological methods of the proportion of larvae in the sea showing symptoms of starvation. If based on adequate sampling, such a proportion could be an indicator of ultimate year-class success.

In March 1977, 64 special net tows were taken over the Southern California Bight from the NOAA R/V *David Starr Jordan*. Net tows, about 3 min long and to a depth of 20 m, were taken with a 1-m net fitted with a quick-release plexiglass cod end. Contents of the cod end from each tow were concentrated in a small seive and immediately fixed in Bouin's fluid.

Three hundred eighteen larvae, about six from each tow, were sectioned and stained with hematoxylin and eosin-phloxine B. The mounted specimens were put in random order and masked in respect to standard length and net tow origin before microscope examination.

HISTOLOGICAL VARIABILITY

Specimens ranging from 2.5 to 10 mm SL showed anomalies in the trunk musculature and notochord, and occasionally also in the pancreas, that closely resembled effects of starvation in laboratory material (O'Connell, 1976). The musculature was considered anomalous if fibers showed some degree of separation, more or less throughout. In the more extreme cases the fibers were widely separated with degraded fibril clarity, and intermuscular matrix tissue was greatly reduced. The notochord in such specimens was usually irregular in profile.

The foregut was considered anomalous if the profile was irregular in lateral view. The mucosa usually showed reduced thickness and variable cell shape. In the worst cases the cells were reduced to little more than the nucleus, and the lumen sometimes contained sloughed cells.

The midgut was judged anomalous when little or no lumen could be traced, or when a traceable lumen was filled with loose nuclei and necrotic debris of mocosa cells with the mucosa proper fragmenting. This kind of dissociation was not observed in laboratory-starved material, perhaps because the laboratory specimens were starved without even having the opportunity to feed, whereas virtually all of the ocean specimens showing symptoms of emaciation had been feeding previously. The midgut thus may have been in a more vulnerable physiological conditon.

Of the 318 larvae examined, 26 were classified as severely or moderately emaciated on the basis of such anomalies. Another 11 were classified incipient emaciation; these are not included in the emaciated or starving contingent.

VARIABILITY OF SAMPLES

In regard to standard length, emaciated larvae were distributed almost proportionately over the range 2–10 mm, but did not occur among larger larvae (some specimens as large as 20 mm were examined). A few of the smallest larvae (less than 3 mm) appeared to be shrunken from a somewhat larger size.

The number of anchovy larvae in the tows varied

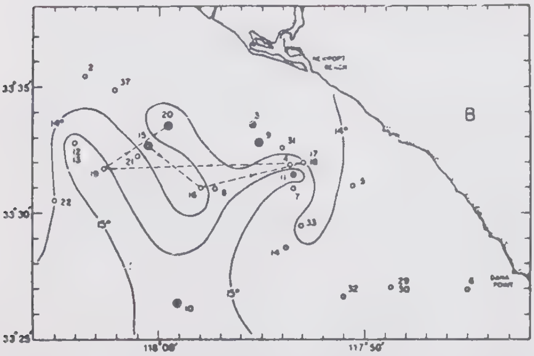

Figure 1. The locations and sequence numbers of tows taken in the Newport Beach area. The larger dark circles with open centers indicate tows with a high proportion of emaciated larvae and the small dark circles indicate tows with a low proportion of emaciated larvae. The isotherms show that there was considerable temperature variation in the area. The dashed line is the cruise track for one 24-h period, and it suggests that the presence of emaciated larvae was a relatively stable feature.

from 0 to 400. Over half of the tows were concentrated in a relatively small area of high larval abundance near shore, while the remainder were spread over a large offshore area where abundance tended to be very low. Some of the emaciated larvae occurred as isolated cases from the offshore-low abundance area, but three-quarters of the total were from six tows from the nearshore-high abundance area (Fig. 1). These concentrations suggest the presence of one or more "patches" of emaciated larvae. Subsequent examination of unsectioned larvae remaining from all net tows strengthened the impression of patches. In tows containing largely healthy larvae, the specimens were full-bodied and regular (Fig. 2). In those containing largely emaciated larvae, the specimens had angular body bends, and trunks and digestive tracts that were lumpy and sinuous (Fig. 3). They were also less intensely colored by the fixing solution.

There was no relationship between the occurrence of emaciated larvae and temperature, but the area where samples with a high proportion of emaciated

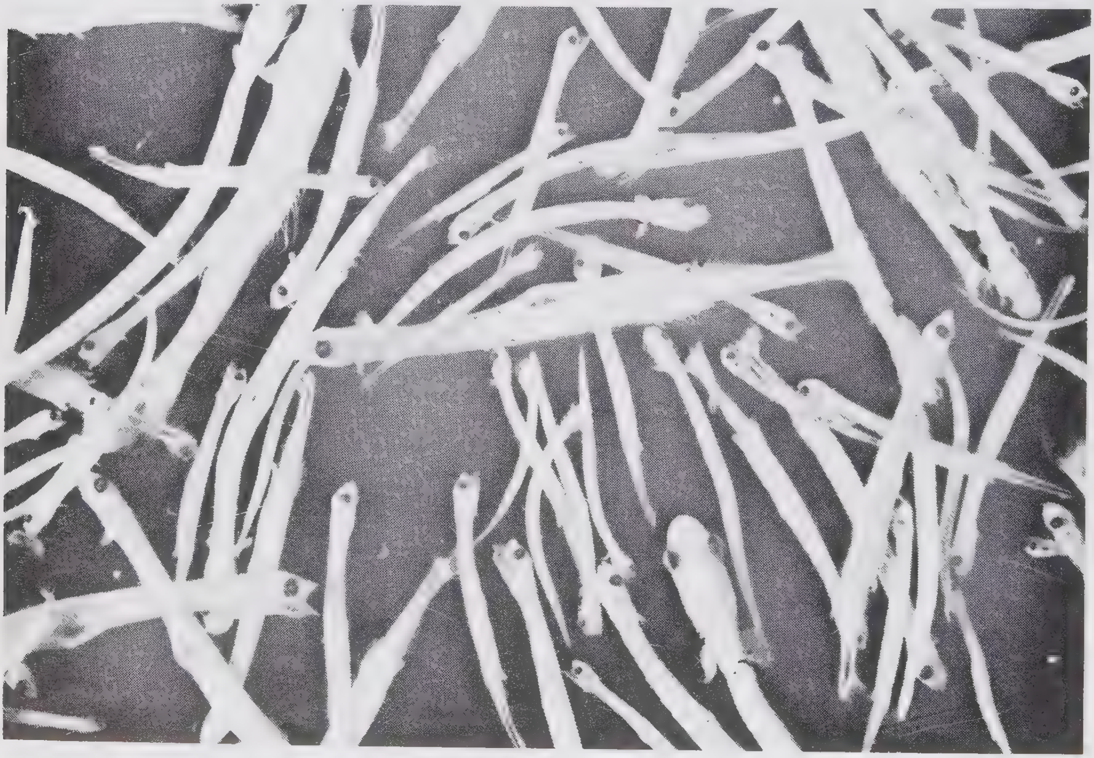

Figure 2. A portion of the larvae from tow 23, which shows generally good body form.

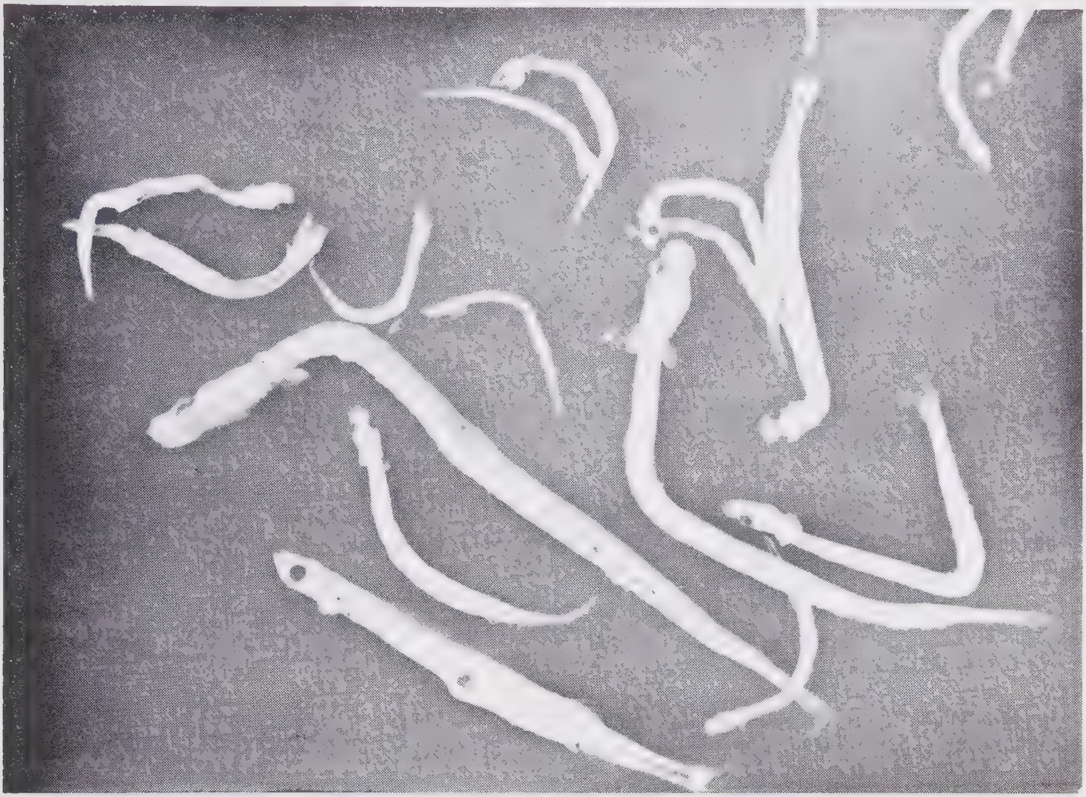

Figure 3. A portion of the larvae from tow 9, which shows generally irregular body form.

larvae occurred was one of considerable small-scale temperature fluctuation.

Number of larvae and plankton volume (larvae excluded) tended to be related for the nearshore samples of high larval abundance (Fig. 4). The tows with a high proportion of emaciated larvae conform to the trend, but they are at the low end of the scale. Plankton volume did vary widely for the offshore samples, but larval abundance tended to be low in all of them.

The proportion of emaciated larvae and other sample data is shown below for the nearshore set of samples, the offshore set, and for the entire cruise pooled.

Sample set	No. tows	Larvae/tow	No. larvae examined	No. larvae emaciated	Percent emaciated	95% confidence limits
Nearshore	37	81.3	220	21	10	±4
Offshore	27	6.3	98	5	5	±4
Total cruises	64	50.0	318	26	8	±3

The nearshore set was distributed over much of the San Pedro Channel area, perhaps 1200 square miles, but it should be noted that most of the emaciated larvae came from four tows in each of which the proportion of emaciated larvae was very high. The offshore set represents an area of perhaps 6000 square miles. The 8% proportion of emaciated larvae for the pooled array tenatively applies to the Southern California Bight as a whole for March 1977.

DISCUSSION

The most significant result of this study is that anchovy larvae showing symptoms indicative of

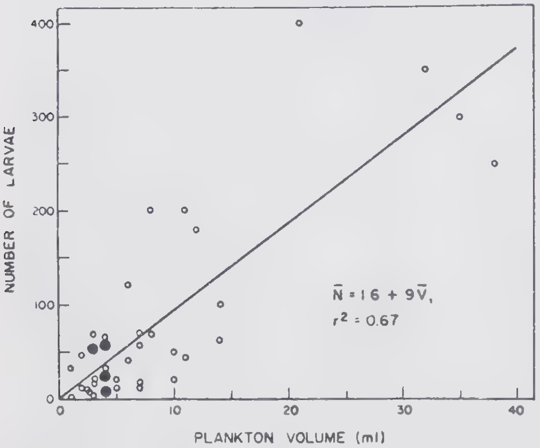

Figure 4. A regression of number of anchovy larvae on displacement volume of plankton (larvae excluded) for the inshore tows, 1–37. The enlarged points indicate the four tows with a high proportion of emaciated larvae.

starvation were found in the ocean, and could be identified on the basis of their individual appearance. The condition of these larvae is similar to that induced in the laboratory by total starvation, which implies that circumstances of insufficient food were responsible for their occurrence in the ocean, especially where samples contained many such larvae. The high variability of plankton volume and temperature in the vicinity of these samples suggests that such circumstances could have existed.

The proportion of larvae observed to be starving may be a useful indicator of ultimate year-class success. It is directly visible and it may reflect a substantial part of total daily mortality of the larvae. Zweifel and Smith (this volume) have estimated that average daily mortality rate for anchovy larvae of slightly less than 10 mm SL in the San Pedro Channel area was 21% over a period of years. The proportion of emaciated larvae in the present survey could be considered a net daily mortality from starvation of 8%, which is 40% of the average daily mortality mentioned above. If starvation contributes this substantially to total mortality, the proportion observed to be starving may relate reasonably well to eventual recruitment.

How well the proportion of starving larvae will relate to recruitment will only be evident from correlation of the two variables for at least a few years. As for the 1977 year-class, a recent estimate from catch data indicates that it is of moderate size, as compared to a large 1976 year-class and small 1974 and 1975 year-classes (Sunada, pers. comm.). Since the 8% starving larvae estimated in this study is associated with a year-class of intermediate size, both higher and lower occurrences of starving larvae can be expected to appear in subsequent years.

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HISTOCHEMICAL INDICATIONS OF LIVER GLYCOGEN IN SAMPLES OF EMACIATED AND ROBUST LARVAE OF THE NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

On the basis of histological criteria (O'Connell 1976), 8% of northern anchovy, *Engraulis mordax*, larvae from special net tows taken in the Southern California Bight in March 1977 were found to be in starving condition (O'Connell 1980). Almost three-quarters of the larvae that showed signs of starvation were concentrated in 4 of the 64 net tow samples. The present report compares the amount of glycogen in livers of additional larvae drawn from these four samples to that in the livers of larvae from samples taken in the same area, which contained robust larvae almost exclusively.

Glycogen, which is stored in the liver and transformed to glucose as needed to maintain an adequate blood sugar level, is the most immediately available of the three energy sources, glycogen, lipid, and protein (Love 1974). It is known to virtually disappear from the livers of many teleosts after only a few days of starvation (Black et al. 1966; Inui and Ohshima 1966; Bellamy 1968), but fish generally live long beyond the depletion of liver glycogen, maintaining the blood sugar level by gluconeogenesis (Love 1974; Cowey and Sargent 1979). However, there are also teleosts in which liver glycogen does not decline sharply at the onset of starvation, although gluconeogenesis does increase (Cowey and Sargent 1979). Thus abundance of liver glycogen cannot be considered a dependable indicator of starvation in teleosts, at least not for adult stages.

Postyolk-sac larval stages, which first exhibit stained liver glycogen about the time yolk is depleted, are more likely to show a drop in liver glycogen at onset of starvation. First feeding northern anchovy larvae die after only a few days of starvation (O'Connell 1976), indicating that reserves are limited. Lipid reserves, for example, are known to be negligible in early postyolk-sac herring and plaice larvae (Ehrlich 1974), and even at the relatively large size of 35 mm SL northern anchovy larvae survive starvation conditions for only 2 wk, on the average, during which time lipid reserves are severely depleted (Hunter 1976). Presumably liver glycogen declines sharply before lipid reserves are depleted in these early stages.

The estimates of glycogen reserves in the works cited above, and in many others, are derived from weight-based biochemical determinations, which is not a feasible approach for small larvae already preserved as part of plankton samples at sea. A histochemical approach is feasible, however, and we elected the periodic acid-Schiff (PAS) procedure, which has largely superseded other histochemical tests for glycogen (Davenport 1960).

Cardell et al. (1973) showed good correlation of PAS staining reactions with biochemical determinations of liver glycogen for the rat. Glycogen decreased from about 9% of liver wet weight to 0.7% after 1 d of fasting and to 0.4% after 3 d. At the start of the experiment all hepatocytes had dense masses of intensely stained glycogen. As the fasting period lengthened to 2 and 3 or more days, the masses decreased in size, number, density, and stain intensity, and the number of cells showing glycogen decreased markedly. Presumably such differences in staining reaction in livers of northern anchovy larvae would be an indication of differences in glycogen reserves.

Materials and Methods

In the laboratory, 49 larvae in the size range 3.5-11 mm SL were selected by random dipping from about half of the 37 nearshore net tow samples that showed larvae of generally good histological condition from the March 1977 cruise (O'Connell 1980). Forty-one larvae were selected, also by random dipping, from three of the four nearshore tows containing abundant larvae in generally poor histological condition. An additional dozen larvae were selected from three of the offshore tows.

All larvae had been fixed at time of capture in Bouin's fluid and stored in 70% ethyl alcohol. They were subsequently dehydrated in *n*-butyl alcohol, embedded in paraffin, sectioned sagittally and stained by the PAS method (Preece 1965). We did not subject the material used in this study to diastase digestion tests but feel confident that the red coloration in the livers indicates glycogen. Glycogen gives one of the stronger reactions to the PAS stain (Lillie and Fullmer 1976), and Cardell et al. (1973) established with diastase controls that the PAS-positive material in the livers of rats was glycogen. The diastase test essentially distinguishes between glycogen and mucins (Preece 1965), some of which show strong PAS reactions, but these occur primarily in the integument and epithelia of the digestive tract and various glands of animals (Lillie and Fullmer 1976).

After staining, slides were randomized with their identities concealed and then rated by microscope examination. Each of two observers rated each specimen as High, Medium, or Low, depending on the degree and extent of red coloration in the liver. The Low grade was assigned when livers showed virtually no red color, the High grade when color was strong and widespread. The Medium grade was assigned when color was light and scattered, or irregular. The two readers disagreed on a little >12% of the larvae but never by more than one grading step. These differences were reconciled by reexamination and discussion.

No attempt was made to characterize the specimens stained by the PAS procedure as robust or emaciated on the basis of histological factors per se. There was the possibility that the PAS procedure would be less precise and consistent than the previously used hematoxylin and eosin stain in demonstrating cell and tissue components other than polysaccharides.

Study of material from the sea samples was preceded by analysis of 99 specimens from groups of larvae that were fed or starved in the laboratory. Fixation, staining, and microscope analysis were exactly as outlined above, except that the laboratory material was held in 70% ethyl alcohol for only a few days before dehydration and embedding. Reader disagreement was 9% on the laboratory material.

The larvae obtained from laboratory containers ranged from 5- to 26-d-old. The rotifer *Brachionus plicatilis* was introduced into containers as food at a density of 40 to 60/ml when the larvae were 3-d-old and maintained above 30/ml by additions as needed. The smaller *Gymnodinium splendens* was included as a starting food at the outset, but was not afterwards maintained. Northern anchovy larvae require *Brachionus* at densities of at least 10 to 20/ml to survive and grow well in laboratory containers for the first weeks of life (Theilacker and McMaster 1971).

Food was withheld from two containers, and specimens from these were sacrificed on the first and second day after yolk exhaustion. Starvation at more advanced ages was accomplished by removing the food from selected containers 2 to 4 d before the larvae were sacrificed. Food was removed with a siphon filter devised by P. Paloma for the purpose. A typical air-driven aquarium siphon was enclosed in an 8.89 cm (3.5 in) diameter perforated plastic cylinder covered by nylon netting with 0.333 mm mesh openings, which allowed food organisms but not fish larvae to pass towards the siphon. The outflow tube of the siphon recurved after passing through the top stopper of the cylinder and terminated in a small perforated cylinder above the water surface. Inside the small cylinder the outflow tube opened into a bag of nylon netting with 0.024 mm mesh openings, which removed food organisms and allowed water to return to the rearing container by dropping onto a small glass plate at the water surface.

Operating at a flow rate of 3 l/h in containers of 12.6 l capacity, the filter reduced *Brachionus* populations ranging from 40 to 100/ml at the start to 7/ml in 1 d, 3/ml in 2 d, and considerably < 1/ml in 3 d. It reduced populations of *Gymnodinium* at about the same rate. At the filtering rate of 3 l/hr, larvae close to the submerged barrier cylinder did not appear to be disturbed.

Results

Laboratory material showed good association between food treatment and PAS glycogen rating over the entire length range involved, 3 to 15 mm SL. The larvae were divided into two groups, those smaller than the median (6.4 mm SL) and those larger than the median. For both size groups, as for all larvae pooled, the majority of High ratings occurred in the "fed" category and the majority of Low ratings occurred in the "starved" category (Table 1). It is noteworthy that only 4 larvae among the 45 from starvation treatments received High ratings. Three of these were from the oldest age group, 26 d (starved 3 d), and were in fact three of the four largest larvae in the entire starved contingent. Examples of stained liver sections representing High, Medium, and Low glycogen ratings are shown in Figure 1.

Larvae from the laboratory trials were fixed in Bouin's solution, as described earlier, to be comparable to the Bouin-fixed sea samples, but a few other fixatives were tested as a matter of perspective. Gendre's solution (Preece 1965) gave somewhat better results than Bouin's, but 10% alcoholic Formalin,[1] which is theoretically a better fixative for preserving glycogen (Davenport 1960; Preece 1965), gave the best results. Some specimens fixed in alcoholic Formalin from fed containers had most hepatocytes solidly filled with deep red color (Figure 1). Presumably more of the glycogen present in the livers at termination was retained with this fixation. However, integrity of cells and tissues of the larvae was not well preserved in alocholic Formalin.

TABLE 1.—Distribution of High, Medium, and Low glycogen ratings, based on PAS staining intensity in livers of northern anchovy larvae fed or starved in the laboratory.

	<6.4 mm SL		≥6.4 mm SL		Pooled	
Glycogen rating	Fed	Starved	Fed	Starved	Fed	Starved
High	14	1	25	3	39	4
Medium	2	7	3	4	5	11
Low	8	18	2	12	10	30

High, Medium, and Low ratings for the ocean-caught larvae (Figure 2) reflect essentially the same levels of staining intensity as for laboratory material. Ocean samples show an appreciably higher proportion of Medium ratings than the laboratory material, but nevertheless exhibit some association between glycogen rating and histological characterization of the samples from which the larvae were drawn (Table 2). However, the association occurs only among the smaller larvae, as indicated by comparing the distributions for larvae smaller and larger than the median, 6.9 mm SL. The smaller larvae show a relatively good proportion of High ratings for robust samples and of Low ratings for emaciated samples. The larger larvae do not exhibit this association.

Significance of the various distributions described above is indicated by X^2 values (Table 3) calculated for each of the six pairs of columns (treated as 2 × 3 contingency tables) from Table 1 and 2. All three X^2 values for the laboratory material clearly reject the null hypothesis, i.e., that there is no association between the two classifications, food treatment and liver glycogen rating. For the ocean material the null hypothesis is rejected only for small larvae, indicating

TABLE 2.—Distribution of High, Medium, and Low glycogen ratings, based on PAS staining intensity in livers of northern anchovy larvae from ocean samples showing either generally robust condition or generally emaciated condition. Condition of samples is based on a previous histological study of other specimens from the same collection.

	6.9 mm SL		≥6.9 mm SL		Pooled	
Glycogen rating	Robust	Emac.	Robust	Emac.	Robust	Emac.
High	7	2	9	8	16	10
Medium	17	5	7	10	24	15
Low	4	10	5	6	9	16

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[1] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

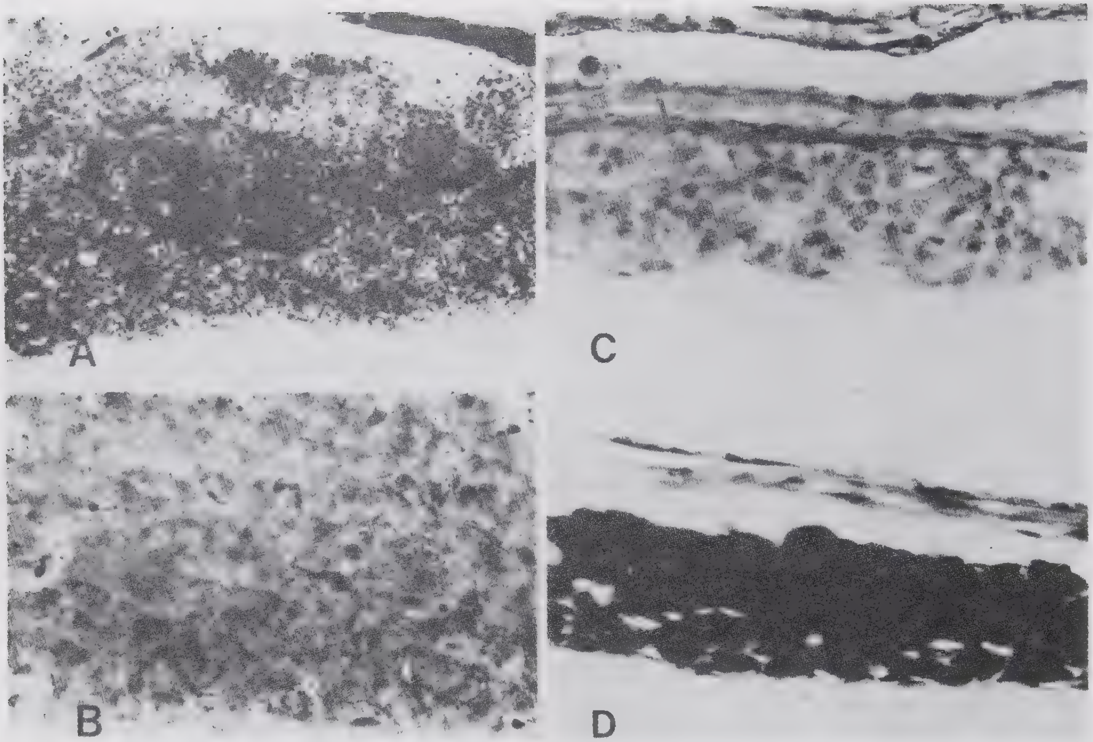

FIGURE 1.—Sagittal sections of livers of northern anchovy larvae from the laboratory, showing the three grades based on intensity of the PAS staining reaction. Except for the nuclei, and occasional portions of other organs, black and the darker shades of grey represent PAS-positive red material presumed to be glycogen. All photomicrographs were taken and processed in the same way. All were taken at 787 ×. A. 5.5 mm larva, fed, graded High. B. 5.0 mm larva, starved, graded Medium. C. 6.1 mm larva, starved, graded Low. D. 5.2 mm larva, fed, graded High. The first three were fixed in Bouin's fluid, but the fourth was fixed in 10% alcoholic Formalin and showed a very intense staining reaction.

TABLE 3.—X^2 and mean contingency square (X^2/n) values for the association between PAS glycogen rating and food treatment for the arrays of larvae shown in Table 1 (laboratory) and Table 2 (ocean). Each set of values is for a 2 × 3 contingency table with (n) larvae and 2 df. In each group, small larvae are those below, and large larvae those above, the median standard length.

Contingency set	n	X^2	P	X^2/n
Laboratory				
Small larvae	50	17.84	0.001	0.36
Large larvae	49	23.28	.001	.48
Pooled	99	40.13	.001	41
Ocean				
Small larvae	43	9.74	.01	.22
Large larvae	43	47	NS	.01
Pooled	86	4.73	NS	.05

that only for the lower part of the length range is there a meaningful association between treatment (histological characterization of the samples from which larvae were drawn) and liver glycogen rating. As already mentioned, the relevant association is High ratings with samples of generally robust histological condition, and Low ratings with samples of generally emaciated condition. The mean square contingency values (X^2/n) indicate the extent to which the association for small larvae from the ocean is weaker than those from the laboratory.

The dozen larvae from the offshore samples, not included in the above analysis of inshore larvae, showed relatively high liver glycogen ratings. They were almost equally divided among three tows, each of which was taken between 0300 and 0400 h on a different day and contained larvae in a different part of the size range. There were no Low liver glycogen ratings among them. Ratings were largely Medium for the small to medium standard lengths (3.4-7.8 mm) and High for the largest larvae (8.0-9.2 mm). These High ratings, moreover, represent the most intensely PAS

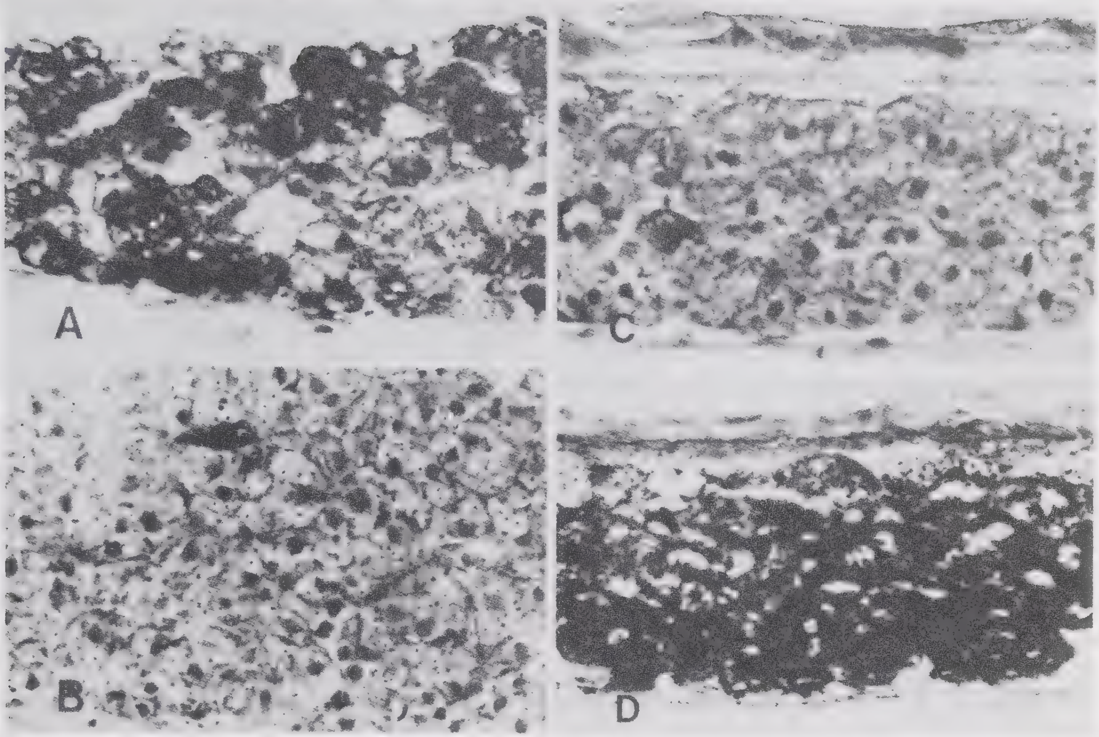

FIGURE 2.—Sagittal sections of livers of anchovy larvae from ocean samples, showing the three grades based on intensity of the PAS staining reaction. Darker shades represent PAS positive red material. Photomicrographs were taken and processed in the same way as those in Figure 1. All were taken at 787 ×. A. 6.2 mm larva, robust sample, graded High. B. 6.3 mm larva, emaciated sample, graded Medium. C. 6.0 mm larva, emaciated sample, graded Low. D. 9.2 mm larva, robust sample, graded High. Whereas the first three are from inshore samples, the fourth is from an offshore sample that produced the most intense staining reactions of all ocean samples.

stained livers in the entire set of ocean specimens (Figure 2).

Discussion

This study was undertaken to determine whether a histochemical test for glycogen in the liver would indicate the occurrence of starvation among northern anchovy larvae from the sea. The results show that variation in glycogen concentration was lower, on the average, for larvae from sea samples classified in a previous histological study (O'Connell 1980) as generally emaciated, than for larvae from samples classified as generally robust. However, the difference was not as strong as it was for larvae that were fed or starved in the laboratory.

Glycogen stored in the livers of fishes can be severely reduced by sustained swimming activity at moderate levels (Miller et al. 1959; Pritchard et al. 1971) or by starvation (Love 1974). It may also undergo some change relative to daily cycles of feeding and nonfeeding. There is no reason to believe that undue exercise was involved in the present case, and the data do not indicate a relation between glycogen rating and hour of capture. Starvation therefore seems the most likely explanation of the low levels shown by certain samples studied here, and this is supported by the relation of glycogen level to plankton volume, a not unreasonable index of food availability in the sea. For those sea samples characterized as emaciated and showing low liver glycogen reserves, the plankton volumes were among the lowest volumes obtained on the March 1977 cruise (O'Connell 1980). These low plankton volumes can be assumed to represent reduced but not essentially nonexistent food, as does the starvation treatment in the laboratory. This difference might account for the greater proportion of Medium ratings in the ocean samples, robust as well as emaciated. In any event, a moderate proportion of Medium glycogen ratings for the ocean samples is not inconsistent with the earlier histological assessments. The emaciated samples, for example, contained only 60% larvae showing histological signs of moderate to severe emaciation or starvation (O'Connell 1980).

The apparently higher level of liver glycogen among larvae from offshore samples further indicates that food availability is an important factor governing liver glycogen reserves. The plankton volumes for all offshore samples averaged considerably higher than the plankton volumes for inshore samples (O'Connell 1980). Moveover, the particular offshore sample that produced the larvae with the most intense PAS indications of liver glycogen had the second highest plankton volume of the entire 1977 cruise.

The fact that the association of glycogen reserves and histological condition is evident for only the smaller larvae from the sea might mean that as larvae become larger, they can better tolerate fluctuations in the plankton regime. There was a hint of this also in the laboratory results. Marine fish larvae in general select progressively larger prey and also a broader size range of prey as they grow, and engraulids tend to increase maximum prey size markedly between 8 and 12 mm SL (Hunter in press). Thus a reduction in any part of the crustacean plankton community, but particularly among the smaller organisms, could be detrimental primarily to the smaller larvae.

The PAS staining procedure appears, then, to be capable of demonstrating the presence of starvation effects in a larval fish population. On balance, it is a more readable indicator than the comprehensive histological analysis, but it also provides less information. The level of liver glycogen reflects the status of only the first line of energy reserve, whereas histological analysis, with more varied indications, is more sensitive to the extent of emaciation that has been sustained by the larva. Perhaps both approaches can be applied to the same larva, but if so, the histological indications should be interpreted cautiously. Our impression is that tissues of larvae can be moderately distorted and degraded by the PAS procedure regardless of feeding history or fixative. On the other hand, the histochemical test might provide a sufficient characterization of the condition of larval fish samples for some purposes, especially if fixation is optimized for the preservation of glycogen.

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MICROSCALE PLANKTON PATCHINESS IN THE LARVAL ANCHOVY ENVIRONMENT

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Spatial sampling of larval fish food at 20 cm intervals was conducted in the Southern California Bight during periods of maximal and minimal spawning by northern anchovy. Microscale variation of food and non-food organism concentrations consistently exceeded sampling and counting error for one or more organism taxons at all but 1 of 14 sites. Sampling casts were made vertically in the mixed layer and pycnocline, and horizontally in the pycnocline. Both motile and non-motile taxons displayed small-scale patchiness. Microscale variation of their concentrations was greatest in the pycnocline on the vertical axis.

MICROSCALE PLANKTON PATCHINESS IN THE LARVAL ANCHOVY ENVIRONMENT

This report summarizes field measurements to determine if small predators and grazers encounter food patches in excursions of less than 2 m extent. Variation in food supply available to larval fish populations is commonly examined to help determine causes of large interannual fluctuations frequently experienced in the availability of fish to fisheries (cf. Sharp, this volume). Yet concentrations of food of first-feeding northern anchovy (*Engraulis mordax* Girard) seem frequently to be too low for larval survival and growth (Lasker et al., 1970). This may be because conventional sampling with plankton nets, which integrate over depth, distance, and volume, has little relation to the comparatively tiny volumes searched by single larvae (Hunter, 1972). Survival of larvae may, in fact, depend on the existence of food particle patchiness on scales considerably less than 100 m and 1 week (Vlymen, 1977).

Sampling sites considered here were in the Southern California Bight, which occupies the center of the usual distribution of the northern anchovy's central subpopulation and of its spawning distribution (Vrooman and Smith, 1972; Smith, 1972). The 14 sites were in coastal waters (bottom depth ⩽300 m) where standing stocks of food particles are usually highest (Lasker, 1978; and this volume) and have been shown to support larval survival during parts of the anchovy spawning period (Lasker, 1975). Sampling was done in March (peak spawning) and in August and September (minimal spawning).

The Southern California Bight is a region tending to high vertical stability by virtue of characteristically slow flow (reduced shear) and year-round net heat gain (except December) by the ocean's upper layer (Clark et al., 1974). The mixed layer usually is shallow (<20 m) or non-existent. Large temperature gradients that predominate over salinity gradients in determining stability, occur in the upper pycnocline in the absence of steady winds. These characteristics are favorable to the development of small-scale patchiness, but are episodically reversed by storm winds which destroy patches.

Samples to assess microscale patchiness at each site were obtained using the device shown in Figure 1. The micropatch sampler (MPS) sampled either in the mixed layer or in the upper pycnocline in the main chlorophyll maximum layer, as defined by pigment fluorescence in a water stream provided by continuously lowered pump and hose. Clamped vertically or horizontally to the ship's hydro-wire and lowered to the depth desired, the MPS captured water at ten intervals on 20 cm centers in 5 cm i.d. tubes of 600 ml capacity by simultaneous messenger-activated release of lanyards which restrained ball valves from their seats at either end of each sample tube. Replicates

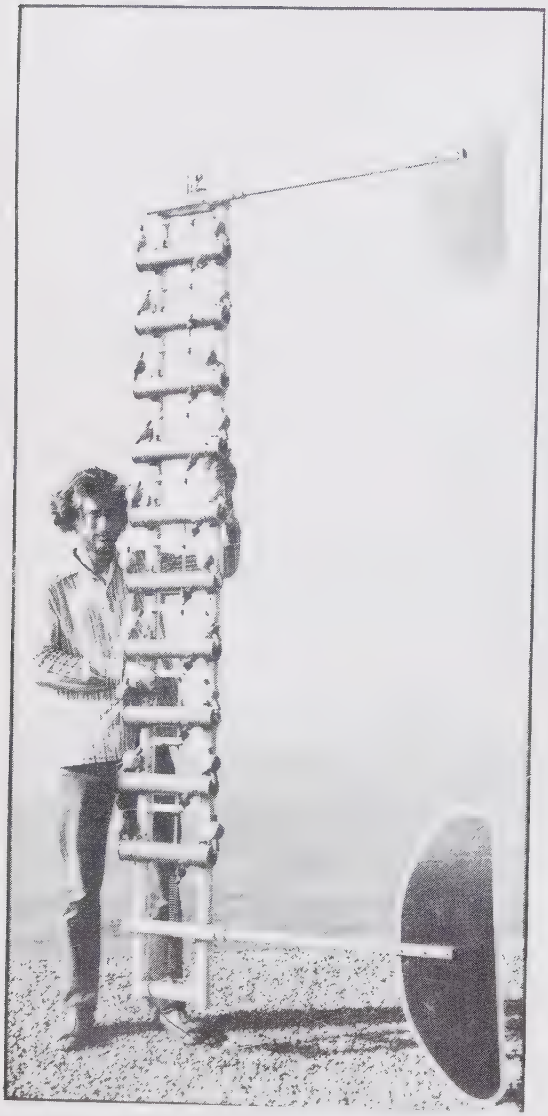

Figure 1. Micropatch sampler (MPS). The array is shown with ball valves open.

were obtained on some casts by strapping another sample tube alongside the original. When sampling vertically, sample tube mouths were oriented by vanes to face a current of ~ 50 cm/sec induced by moving the ship slowly ahead. This minimized vertical mixing of the water by the MPS. When sampling horizontally (tubes vertical), the tubes were closed while raising the array into water disturbed only by the ship's wire. Water thus obtained was aliquoted for various analyses from the well-stirred contents of the MPS tubes upon recovery aboard ship. Samples for microscope analysis were preserved in 5% buffered formalin spiked with strontium chloride. These were counted ashore by the sedimentation method of Utermöhl (1931).

Results of microscope counts are summarized in Table 1 as coefficients of variation, V = 100 · variance/mean, of concentration over the 10 intervals sampled to represent the 1.8 m span. Where replicate samples were counted, average values between replicates were used in the computation. Coefficients are shown for population counts exceeding 10 in at least one of the samples in the set. Trends (i.e., mean gradients) over the 1.8 span are represented by the coefficients, as are variations within the span (i.e., deviations from mean gradients), both sources are taken to indicate microstructure degree because sampling was done in the absence of detectable macrogradients (i.e., in mixed layer and chlorophyll maximum). The V statistic was chosen not because it is necessarily the most appropriate, but because it scales variances for comparability and because it is widely used and understood. A measure of sampling and counting error is provided from counts on four MPS sets each consisting of five replicate sample pairs. The average coefficient of variation between replicates for 15 taxonomic groups counted was 10.9 (range was 4.0–18.5), not including the coefficient for ciliates associated with marine snow at two sites (7703J-MS1, MS2).

Considering interval V-coefficients to indicate a significant degree of microstructure if they exceed replicate V-coefficients by at least a factor of 3, Table 1 shows that:

1) Microscale patchiness is apparent (V ≥ 33) at all but one of the fourteen Southern California Bight sampling sites for one or (usually) more kinds of organisms enumerated;

2) Most types of organisms suitable as larval anchovy food display significant degrees of microaggregation. Non-food organism types are also aggregated, in many cases to an even greater degree, and not necessarily in the same zones as food organisms (Fig. 2);

3) Vertical profiles in the upper mixed layer (the latter defined by absence of density gradients determined from standard STD casts) showed significant microscale patchiness for 5 of 8 food types and 3 of 8 non-food types at one site or the other, both occupied during the anchovy spawning season under calm wind conditions;

Table 1. Coefficients of variation of organism concentrations sampled at ten 20-cm intervals (interval replicates averaged where obtained) in the mixed layer and upper pycnocline of the coastal shelf of the Southern California Bight.

	Vertical casts in pycnocline at chlorophyll maximum layer								$\overline{V}$	Horizontal casts in pycnocline			$\overline{V}$	Vertical casts in mixed layer		$\overline{V}$
Top depth (m):	22	23	25	29	20	20	14	20		17	18	21		10	10	
Date (year/month):	75/09	75/09	75/09	75/09	76/03	76/03	77/03	77/08		76/03	76/03	76/03		76/03	77'03	
MPS no.:	1	2	4	5	1	5	2	1		3	10	11		2	1	
Food Types																
Exuviaella sp. C					22.7	17.3				27.4	29.1	21.8		12.8	76.6	
Oxytoxum septrum						27.7										
Prorocentrum gracile	69.8	52.6	138.4		45.4									37.6		
Peridinium (2 spp.)					50.9						19.2			25.4		
Peridinium minutum					174.1		25.0				35.2			35.5	21.2	
Cochlodinium catenatum	28.4		51.2	44.9				22.0								
Gymnodinium sp. S					22.2											
Torodinium robustum								29.8								
naked flagellate 30x50 μm					67.4			14.5		27.3	21.4	17.3			41.6	
tintinnids						98.6								22.2	34.2	
free ciliates			54.6	44.2	64.1	11.5	63.2			26.2	14.3	24.4		9.9	23.4	
copepod nauplii					32.0	25.4					29.6			10.7	31.8	
$\overline{V}$									49.9				24.5			29.5
Non-Food Types																
Nitzschia seriata					51.8	44.9					35.7			29.2		
Eucampia zoodiacus							115.7							31.0		
Thalassiothrix frauenfeldii														25.1		
Thalassiosira sp. A							27.3									
pennate diatom 30 μm			158.2	92.2												
silicoflagellate			55.3	60.4												
Ceratium kofoidii	39.1				58.4					39.2						
dinoflagellate spp. 5x10 μm					27.9						31.1			27.0		
Pseudoeunotia doliolus	95.7	104.6	56.8													
Thalassiosira sp. B								28.9				37.3				
Skeletonema costatum														40.1		
pollen grain 70x40 μm															65.6	
oikopleurans														52.4		
Noctiluca sp.					29.0	21.2					24.2			21.5		
$\overline{V}$									62.8				33.5			36.5

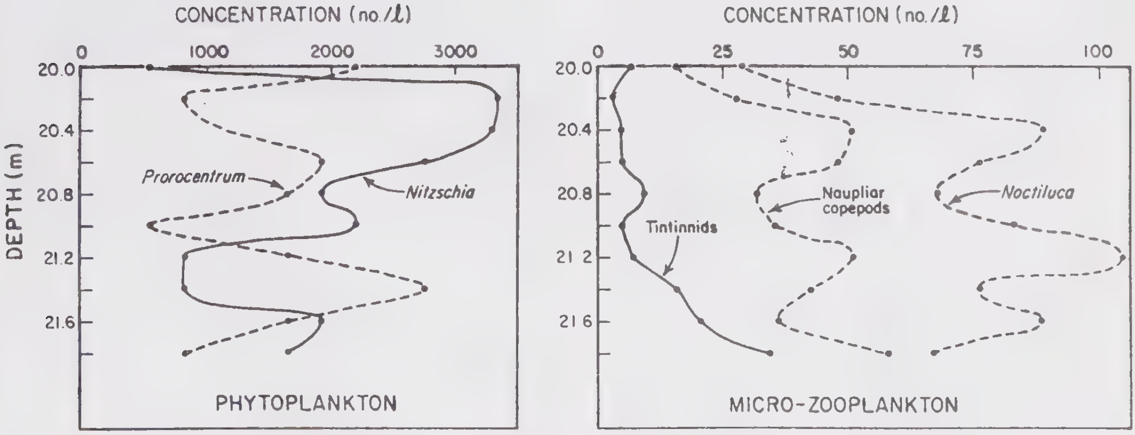

Figure 2. Variation of concentration of microplankton in samples from 20 cm depth intervals in the pycnocline (vic. depth of the main chlorophyll maximum) in March 1976 over the coastal shelf of the Southern California Bight (7603J MS1). *Prorocentrum*, tintinnids and copepod nauplii are larval anchovy food items.

4) Microscale variation was usually greatest in the pycnocline and in the vertical axis for most food and non-food types alike (but see *Exuviaella* sp. C — this flagellate species behaves rather differently on the microscale, being more randomly dispersed vertically than horizontally in the pycnocline and apparently capable of forming small patches in the mixed layer);

5) Horizontal variation was usually less than vertical variation in the pycnocline, indicating (except for *Exuviaella* sp. C) lenticular patching and anisotropic behavioral or physical processes that control patchiness;

6) Non-motile or weakly motile organisms (cf. *Nitzschia*, *Thalassiosira* and pennate diatom categories) may show as much or more patchiness as motile organisms (cf. *Exuviaella*, *Prorocentrum* and ciliate categories);

7) There is no evidence for a difference in degree of microstructure between periods of peak and minimal spawning activity (mean V = 49.9 and 50.1, respectively). This is perhaps partly due to too few comparable categories since species composition changed between the two periods sampled.

Microscale variations reported here are due to two sources beyond sampling and counting error. First, free-living organisms aggregate by active (behavioral) or passive (physical) mechanisms. Second, some food-type organisms associate with macroscopic particle aggregations (Silver et al., 1978; Alldredge, 1972) When such colonized aggregates are large and dispersed *in situ*, they are likely undersampled by the MPS, giving rise to increased variation when they are disintegrated by sample manipulation prior to analysis. Distinction between these two sources of variation is difficult without direct observation, but is important because organisms associated with marine snow are available for grazing by a rather different set of predators than are free-living organisms. In particular, first-feeding anchovy larvae are not known to pick at macroscopic aggregates, and their mouths are too small for complete ingestion of whole aggregates larger in least dimension than 200–250 μm (Hunter, 1977). From this set of samples, presence of large aggregates was detected by uncharacteristically large disparity in counts of ciliates and detritus from replicate samples during March 1977, both in pycnocline (7703 MS2) and mixed layer (7703 MS1).

A second point not apparent from Table 1 is that maximum concentrations of food and non-food organisms do not usually coincide on the microscale. A characteristic experience is shown in Figure 2, taken from a vertical MPS cast in the pycnocline, in the vicinity of the main chlorophyll maximum. This effect may augment the increase in availability of food organisms due to microstructure by local clearing of undesirable strike targets in zones where food organism concentrations are highest. This argument assumes varying degrees of desirability among the food types, as there are no consistent patterns between total food and non-food organism distributions on this scale.

Concentrations of suitable food at one site (7603 MS1) of the 14 reported here exceeded the "critical concentration" criteria of Lasker and Zweifel (1978) for survival and growth of anchovy larvae. This incidence would likely be higher if (1) all food type organisms had been enumerated or if (2) plankton richness had been among criteria for choosing sampling sites.

The observations reported here to date suggest no simple relationship between organism types, but show a large degree of variation on short intervals. Results confirm Vlymen's (1977) postulate that small-scale patchiness (on the order reported here) must necessarily occur to support even the minimum fraction of anchovy larvae surviving to recruitment size. The results also suggest sampling precautions to be taken wherever minimum or maximum plankton concentrations need to be known or where "critical concentrations" need to be detected.

This work may thus be applicable to populations other than that of the northern anchovy. Populations of *Anchoa* and *Achirus* are held to be food-limited at the larval stage (Houde and Schekter, this volume) as well as of North Sea haddock (Jones, this volume). The argument may also extend to such grazers and predators as copepods (e.g., Marshall and Orr, 1955, p. 97).

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7 Fronts and Eddies in the Sea: Mechanisms, Interactions and Biological Effects

ROBERT W. OWEN

1 Introduction

This chapter concerns fronts and eddies, two major classes of water motion that create and change patterns of biological distributions. Flow of water across topographic features in the open sea produces patterns of vertical circulation ('fronts') and eddy-like motions which can reorder life processes and distributions in a variety of ways. Such patterns may also arise independently of sea bottom topography from ocean current confluence, from wind stress applied unevenly in space and time, or from heat and water exchange across the sea surface. Frontal and eddy circulations can occur at any depth and affect populations of organisms at all trophic levels, including benthic forms from great depths to the littoral zone. Life forms as diverse as phytoplankton, protozoans, crustaceans, fish, sea snakes, marine mammals and birds are found to alter their distributions in the presence of such flow patterns.

The ocean is widely held to be turbulent upwards of the scale of a few centimeters and seconds, but also to contain quasi-ordered velocity fields. Recent experimental work suggests that such ordered fields may be more prevalent in turbulent fluids than previously believed (Laufer, 1975). Fronts and eddies are two such classes of quasi-ordered velocity fields. We are concerned here with flow patterns that locally alter biological distributions, but it is obvious that various processes causing fronts and eddies can occur at the same place and time. This frequently leads to a degree of complexity that approaches fully turbulent motion, i.e. chaos. To the degree that organisms interact with mixed regimes of physical processes, patchiness of organisms induced by behavioral mechanisms alone may be obliterated.

There is a considerable body of evidence that patterned patchiness frequently arises from patterned circulation. Environmental circumstances under which such patterns arise are often rather unexceptional, and thus may be more widespread than case studies imply. There is also some promise of prediction of patterning (or de-patterning) circulations, which would be of value in estimating yield of fish stocks affected by patterning of food and supply. Accounting for such patterning of organisms, which is recurrent and widespread in many instances, should also enhance the accuracy of biological production models constructed for organisms at any position in the food web.

Fronts and eddies are engendered by a variety of physical processes and have a variety of biological consequences. The terms 'front' and 'eddy' are used here to denote localised zones where quasi-ordered singularities of lateral flow induce or intensify vertical flow. A front is a line or linear zone that defines an axis of laterally convergent flow, below or above which vertical flow is induced (Fig. 1). A frontal system denotes sets of convergences. These usually produce alternating zones of downwelling and upwelling flow. An eddy denotes an area of closed horizontal streamlines where vertical motion is induced or sustained.

Fronts and eddies are recurrent or persistent singularities in the ocean's usually turbulent flow. They are found singly, in groups, and in combination in all seas and at all depths, although most frequently and to clearest ecological effect in the surface layers. Characteristic motions have been detected on scales that range from 1 to 10^5 m laterally and 1 to 10^3 m in depth, and persist from a few hours to virtual permanence. The magnitude of ecological effects, however, is not necessarily scale-dependent. Time and space scales are related: the smallest fronts and eddies are the most ephemeral and the largest are the most permanent. This relationship holds because driving forces are more ephemeral on small scales, because size of circulations tend to increase where the driving force is maintained, and because when the driving force relaxes, larger circulations persist longer.

A basic and attractive tenet implicit in much of the work in this area is that vertical displacements have greater ecological effects than similar horizontal displacements because environmental gradients, such as light, pressure, temperature, salinity, oxygen, nutrients and flow, are by far the steepest in the vertical (chapter 14). Vertical motion in fronts is often vigorous and highly localised, whereas in eddies it is slow and spread over much larger areas. For this reason, lateral gradients of temperature, salinity and food supply are correspondingly sharper across convergent flows than across eddies. Direct responses of organisms have not often been demonstrated, and causal effects are notoriously difficult to isolate.

Vertical motion in eddies occurs to compensate for lateral flow into or out of the circulation. Such convergent or divergent lateral flow occurs as a result of deflection due to the Coriolis parameter of relative motion on the rotating earth (Von Arx, 1962). Cyclonic eddies of sufficient size exhibit divergent flow due to the Coriolis deflection and compensatory upward movement occurs. Anticyclonic eddies, conversely, exhibit downward

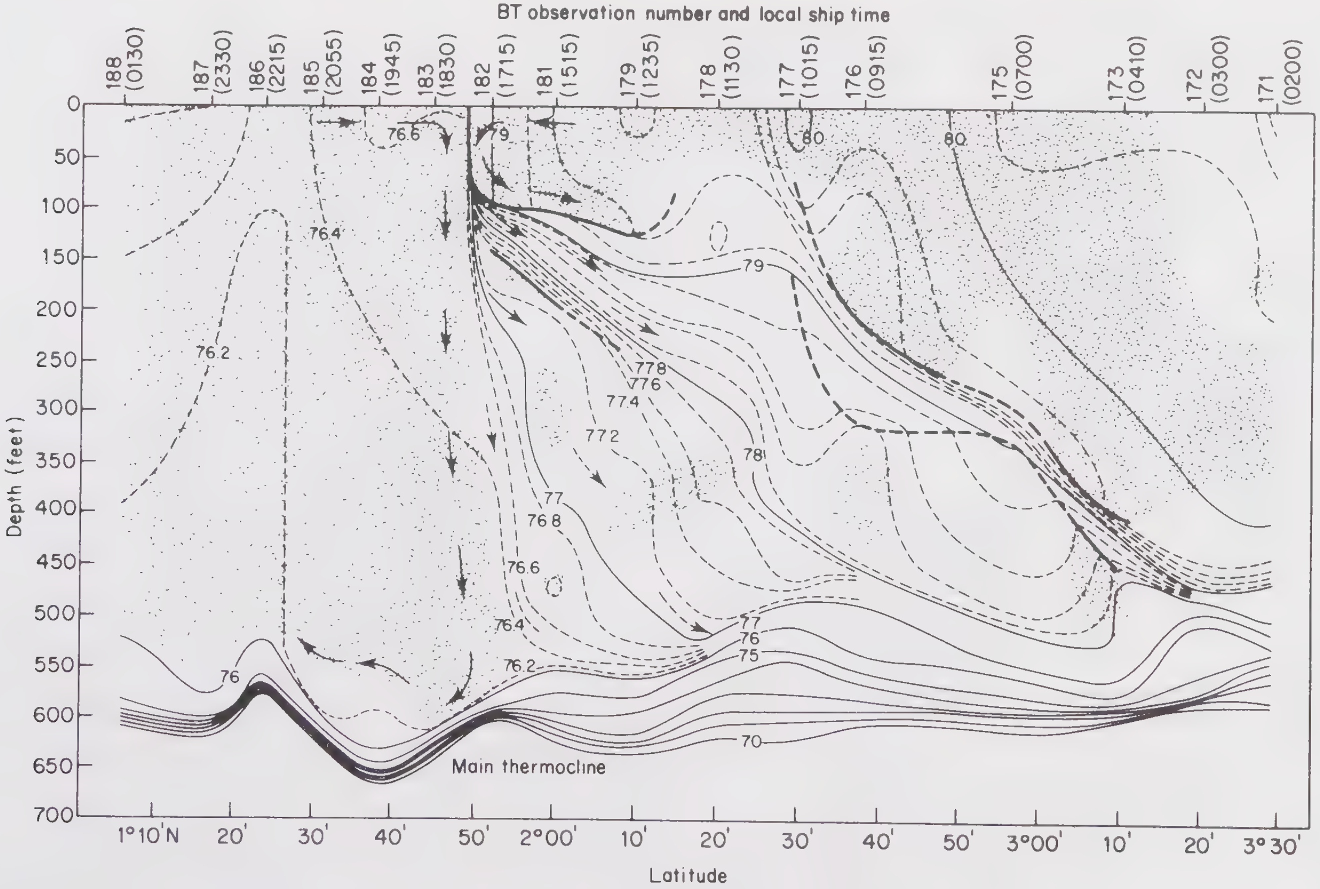

FIG. 1 Thermal structure and inferred circulation in an ocean front along 172 W near the Equator. From Cromwell and Reid (1956)

motion in their interiors. Estimates of upward velocities in large cyclonic eddies (cf. Owen, 1980) are of the same order as sinking rates of some phytoplankton and detrital particles and can also transport substantial nutrient supplies upward (Broenkow, 1965). Whether cyclonic or not, eddies are zones of horizontal recirculation and thus locally maintain and transport their contained populations and substances.

Difficulty of detection and measurement at sea in part accounts for the fact that we can only guess at the full extent, nature and ecological impact of some of the interactions reviewed here. We currently look to advances in instrumentation and observation platforms (especially appropriately equipped and deployed spacecraft) to add needed perspective and we regard the study of such singularities to be in its early stages.

2 Interactive characteristics of organisms and substances

Most macroscopic particles, living or not, have properties that make possible their differential concentration in the presence of fronts or eddies of appropriate scale and intensity. These properties are: differential motion (sinking, floating and swimming) and proliferation (production and reproduction). Characteristics of these properties are more or less specific to the type of particle. They operate interactively with vertical circulations either directly or indirectly as rates and directions of sinking and swimming and on local rates of production. Rates and directions are in turn responsive mainly to food (or nutrient) supply and to environmental gradients, especially light, temperature and food concentrations.

It must be emphasised that a degree of randomness is typical of both water motion and organism characteristics. Sinking and swimming rates vary between organisms of the same species, size or population, and water motion is usually subject to random variations so that trapping efficiency of a particular circulation is accordingly diminished, as is the sharpness of the resulting patterns of organism concentration. It seems clear from case studies, however, that factors creating pattern frequently predominate over those that disrupt it. Vertical movement, for example, tends to be more consistent in rate and direction among individuals of the same types than among individuals of different types.

The same arguments apply to production rates: among plankton species represented at a site, several are likely to respond with similar division rates to a change in, say, nutrients supplied by a front or eddy. Such species become differentially concentrated as a set if their vertical motions are either similar or not important. Production rates tend to be more similar within than between organism types, ranging upward to 2 doublings/day among some phytoplankton populations.

Particle characteristics that determine sinking rates are size, form and density. Volume and density of a particle govern its buoyant forces whereas its surface area and form are the primary determinants of local fluid drag.

Detrital particles of filterable size sink in still water at rates depending primarily on their size and form. Detritus is predominantly microscopic but can exceed 1 m in largest dimension in shapes as diverse as "burst balloons", strings and sheets. These can have occluded bubbles and lumps that make estimates of density and sinking rate uncertain. The bulk of detritus, however, has little apparent potential for passive collection except in the slowest convergences and perhaps in cyclonic (upwelling) eddies. This is because most detrital particles sink slowly: they are either quite small or are in an aggregated form known as 'marine snow'. An important exception is fecal pellets of zooplankton, particularly those of copepods since they are so numerous. Smayda (1969) found still water sinking rates of naturally occurring fecal pellets to range from 1.5 to 15.6 m h^{-1}, mostly about 6 m h^{-1}. Large pellets sank faster than small ones, and shape effects also were discerned. Effects of diet on pellet buoyancy and shape are apparent from observations of Marshall and Orr (1955) and may be expected to influence sinking rate of the pellets. Disintegration and bacterial or fungal growth probably affect sinking rates of older pellets.

Sinking of diatoms, which have little or no other motility, was reviewed comprehensively by Smayda (1970). He cites sinking rates up to 1.26 m h^{-1} for a large centric diatom and average rates of about 1 m day^{-1}, determined on live cells sinking in still water. Smayda also cites studies of sinking rates derived from field observation of rates at which diatom layers changed depth. These ranged from 1–5 m day^{-1}, greater than still water sinking rates of the same or similar species.

Many diatoms apparently exercise a degree of control over their sinking rate through regulation of their density, size and shape. Changes in sinking rates favorable to the population have been noted to occur in apparent response to environmental factors, notably light and nutrient levels. although sinking predominates widely, diatoms may also become positively buoyant on occasion, changing buoyancy by ionic regulation of cell sap density or by accumulation of fats. Smayda (1970) cites several cases of centric diatom blooms at the sea surface that dramatically demonstrate floating. As would be expected if cell density were independent of its volume, the main influence on still water sinking rates of phytoplankton is cell size (or aggregate size, if colonial). Eppley *et al.* (1967) summarise this effect and also emphasise the physiological condition of cells as a determinant of sinking rate. Cells from senescent cultures sink about four times faster than cells from growth-phase cultures. Increased sinking rates would place nutrient-deficient or light-blitzed cells at water depths more favorable in either respect.

The determination of sinking rates in dinoflagellates is more complex because most are motile. A passive sinking rate of *Gonyaulax polyedra* in growth phase was reported by Eppley *et al.* (1967) at 2.8 m day^{-1}, whereas swimming at 1 to 2 m h^{-1} is indicated by studies of this and other dinoflagellate species (Hasle, 1950, 1954; Hand *et al.*, 1965). In any case, dinoflagellates move faster by swimming than by sinking.

Phototaxis is not restricted to dinoflagellates, but is widely represented among motile plankton and fish species. The resulting diel patterns of vertical migration thus occur in every phylum represented in the sea and for a wide variety of apparent advantages to the migrants. Longhurst (1976) provides a recent discussion of the mechanisms and advantages of vertical migrations as well as entry to the extensive literature on patterns of vertical movement of zooplankton. In circumstances where phototaxic migrants move into or through persistent vertical circulations, patterns due to their interaction must necessarily have diel periodicity. Zones of higher organism concentration in daylight would thus become rarified at night, as the migrators would instead collect, if at all, at convergences of the opposite direction. Diel variation of convective circulation in the surface layer (Woods, in press) also would affect such patterning.

Hardy and Bainbridge (1954) measured swimming speeds of various zooplankters by placing individual animals in a water-filled torus, which was then rotated on its horizontal axis at recorded rates to keep the swimmer at the same height. Sustained upward rates of nearly 30 m h^{-1} were achieved by the robust copepod, *Centropages*, and 90 m h^{-1} by the euphausiid, *Meganyctiphanes norvegica*. Downward speeds often exceeded upward speeds: e.g. *Calanus* sustained speeds of 47 m h^{-1} downward versus 15 m h^{-1} upward. Enright (1977), from open ocean catches of the 2–3 mm copepod *Metridia pacifica* in several sets of serial net hauls made vertically above and below the base of the thermocline, determined upward swimming speeds from 30 to 90 m h^{-1} for more than an hour. This was greater by 2 to 10 times than previous field estimates he noted. These values give some idea of the maximum depth range that could be traversed in one or two hours of vertical swimming in the absence of vertical flow.

Sinking rates of zooplankton are usually small compared to their vertical motility, but could be important during periods of inactivity. One such period is at night: after the organisms have completed their main upward migration, passive sinking may occur for several hours before downward migration is induced near dawn (Raymont, 1963). Sinking has been invoked to explain the 'midnight scattering' apparent among various vertical migrants that spend the night in the upper layer. This scattering could as well be due to random vertical swimming in the absence of light stimulus. Midnight scattering may be followed by upward swimming near dawn just before the migrants swim downward to seek their daytime levels.

Diel vertical migrations of fish usually follow the pattern of most zooplankton migrants; rising to the surface layers around sunset, dispersal during darkness, and returning to deeper layers by sunrise. Adults and larvae of sardine, herring, pilchard, coalfish and plaice have been noted to migrate roughly according to this pattern, and many myctophids and gonostomatids perform regular diel migrations to the sea surface layer from several hundred meters depth. These larger zooplankton and fishes do not necessarily interact directly with patterning circulations, but may find feeding advantages where their prey are so concentrated.

Organisms not directly affected by patterned vertical motions may nevertheless respond to substances or to organisms that are so affected. For example, nutrient salts brought up to the euphotic zone locally stimulate production of phytoplankton, whereas zooplankton patterned by vertical motion may locally graze down phytoplankton or attract predators, producing secondary patterning of either. Similarly, flotsam and surface active materials collect at surface-convergent fronts where they subsequently can attract or affect organisms. Some, if not most, organisms respond selectively to gradients that are created or modified by fronts and eddies.

Attraction to food commonly accounts for aggregation of animals at or near fronts larger than the Langmuir pattern. They may arrive by a variety of ways. Passive floating behavior by *Pelamis platurus*, the sea snake, causes large aggregations at fronts in the eastern tropical Pacific where they feed on small fish (Kropach, 1975). Small fish, in turn, aggregate in these fronts for plankton. Several species arrive with the floating wood and debris to which they are attracted (Hunter and Mitchell, 1967). The phenomenon is commonplace and commonly attracts larger and smaller animals of recurrent species, leading Dunson and Ehlert (1971) to suggest that the fronts create a community. Most often seen nearshore, such assemblages occur in offshore water to sometimes dramatic degrees. In the offshore eastern tropical Pacific, fronts occur that assemble plankton, fishes, birds, whales and porpoises, as well as flotsam with expatriated littoral and neritic animals and plants. Beebe's (1926) classical description of such a front lists several species in each of these categories. They arrived in numbers by every conceivable pathway.

These observations have been since confirmed and extended, e.g. for bird aggregation by Ashmole and Ashmole (1967), and for mammals by Gaskin (1968 and 1976). Food aggregations were the attractants in each case.

3 Patterned flow types, scales and genesis

Where circulation characteristics are determined by the presence of coastlines, islands, banks, seamounts, etc. the pattern is under topographic control. Circulations under dynamic control are relatively independent of topography, and include fronts and eddies arising from atmospheric forcing and from current confluence, meandering, or other flow instabilities. Fronts and eddies of both types occur at all sizes and frequencies important to organisms. Those of the dynamic type occur virtually anywhere in the sea, whereas the topographic type occur most frequently and noticeably along continental margins and in island wakes.

Due to their proximity to external driving forces, the surface layers of the sea tend to be the most energetic, both physically and biologically. Topographic control is thus most pronounced where the bottom is shoal enough to intercept and modify surface layer processes. Although active over far less ocean area than dynamic processes, topographic fronts and eddies operate in zones already high in biological activity. Fronts and frontal systems that affect measurable biological conditions operate on scales as small as meters and hours and as large as 10^3 km and years. On the other hand, eddies of less than a few km in radius and a week in duration have not been noticed to produce biological patterning. Although small eddies transport and perhaps conserve materials, their main effect is to broach or attenuate features of larger scale and thus act more to disrupt than to create pattern.

SMALL-SCALE FRONTAL SYSTEMS

Patterned convergences on the smallest scales at the sea surface are usually accounted for by cellular convections due to wind or to thermocline effects. Such convections take the form of paired, vortical cells of opposing rotation around their horizontal axes. Water downwells where surface flow converges between cells and upwells where subsurface flow converges. Thermohaline convection occurs when denser water forms rapidly at the sea surface and is responsible for the smallest patterns seen to collect organisms. Denser water forms by cooling due to evaporation, back radiation and heat conduction from the very surface. The density increase by cooling may be augmented by the salinity increase from evaporation. Formation of denser water at the sea surface creates vertical instability. At high rates of formation, this water is hydrodynamically most easily discharged by sinking of the dense water along preferred planes rather than by simple diffuse sinking as small filaments. This process has been observed to create patterns of small-scale convection cells which are elongated Bénard cells. Bénard cells may be commonplace under light wind conditions and probably augment convection at higher wind speeds. Defant (1961) reviewed criteria for such convections and gave evidence that Bénard circulations are frequent and widespread in equatorial and mid-latitudes, extending in depth to 25 m or more in the absence of overriding motions. Instability of surface layers, due mainly to evaporation, is cited to occur in the entire pelagic sector of the Atlantic from 20°N to 50°S and to be most pronounced between 15°S and 20°S.

The smallest coherent frontal patterns that have been noted to collect organisms in the open sea were attributable to the Bénard mechanism. Surface convergences penetrated to less than a meter in depth, extended visibly for more than 30 m in unbroken length, spaced at intervals of about 1.5 m. The patterns persisted in the absence of wind for at least two days (Owen, 1966). Taken singularly, such 'micro-fronts' would have little ecological impact. This particular frontal system, however, extended over several hundred km^2, so that even such fine-scale patterns can produce widespread alteration of concentration patterns and, presumably, concentration-dependent biological processes. In this instance, the surface convergences were marked by red bands less than 10 cm wide that consisted of upward swimming oikopleurans that had been highly concentrated in the upper 5 cm of the convergence planes. Their still water swimming speed of about 0.2 cm s^{-1} set an upper limit on downwelling water speed in the convergence planes.

Under freshening and sustained winds, convergence systems of the better known and (usually) larger scale Langmuir circulation either develop extant Bénard cells or create their own patterns, detectable as parallel windrows. Windrows lie along the wind axis and are often marked by assemblages of any floating (i.e. strongly buoyant) substances in the neighborhood. These are swept by convergent surface flow to the frontal zones. Trapping efficiency of buoyant materials is virtually 100% under steady wind direction. Surface convergences can become strong enough on occasion to submerge even highly buoyant *Sargassum* weed, requiring a downwelling circulation of 5–7 cm s^{-1} (Woodcock, 1950). Organic films on the sea surface also are rapidly collected along such convergences to give windrows their characteristic banded appearance. Under lower winds, collected oils dampen capillary waves to give the windrows the appearance of parallel slicks. At higher wind speeds, the organics are partly frothed and mark convergences by foam lines.

The size and circulation strength of these convection cells increase with time and wind speed. Spacing of convergence lines several meters to over 100 m is typical, and downwelling speeds may exceed 10 cm s^{-1}. Depth of penetration is some fraction of the distance between convergences, usually half or somewhat less.

Extant theories that attempt to account for the Langmuir circulation include instability of vertical shear in the water, forcing by atmospheric vortices, wind-oriented thermal (Bénard) convection, wind profile modification by surface films, lateral radiation pressure on surface films, convergence of wave trains (reviewed by Scott *et al.*, 1969), and vertical decay of surface wave oscillations (Faller, 1969). Failure of their data to support or rule out any single mechanism led Scott *et al.* (*op. cit.*) to conclude that combinations could occur of mechanisms they considered. A subsequent study (Harris and Lott, 1973) lends support to the possibility of development of Bénard cells into Langmuir cells: mean downwelling velocities ranging from 2 to 10 cm s^{-1} in Langmuir convergences correlated well with wind speed during net surface cooling but not as well during net surface heating. Despite the lack of agreement on mechanisms, Langmuir circulations are now widely held to be the most important mechanism for vertical transfer of heat and substances in surface waters of lakes as well as oceans.

The theoretical and mathematical description of particle trajectories in cellular convections was formulated by Stommel (1949) and subsequently elaborated to include swimming (e.g. Stavn, 1971). Direct observations confirm the applicability of the model to real particles and plankters in such circulations, despite the rather large difficulties of field measurement and the less-than-ideal behavior of both the fluid and plankters.

A number of field studies confirm the effectiveness of the Langmuir circulation in collecting and patterning organisms and substances. The most visible examples involve buoyant animals and substances such as *Physalia* (Woodcock, 1944), *Sargassum* weed (Faller and Woodcock, 1964; Woodcock, 1950) and surface films (Szekielda *et al.*, 1972). Sutcliffe *et al.* (1963) demonstrated that whitecapping and perhaps other wind action converts dissolved organics to particulate form available to zooplankton, and that a Langmuir convection downwelling at 3–6 cm s^{-1} produced subsurface concentrated zones of these particulates. The soluble inorganic phosphate concentration was also shown to be higher in such particulates. Sutcliffe *et al.* (1971) showed, by detecting an increase in particle concentrations with increase in wind speed, that the process is highly effective. They found peak production to be particles of 6 μm diameter. Higher concentrations of particles 2–13 μm diameter were found below convergence zones.

Patterning of phytoplankton and microzooplankton by Langmuir circulations has been more widely reported than one would expect from the mismatch of their reported rates of vertical motion. Bainbridge (1957) reviews several observations of dinoflagellate concentrations in Langmuir-scale patterns. The mobile and prolific ciliate *Mesodinium rubrum*, which can occur in blooms ('red-water') concentrations, has been reported to gather in Langmuir convergences. Powers (1932) found them in windrows off Maine, and Bary (1953) found windrows of the same ciliate to orient along a changing wind axis in New Zealand. Packard *et al.* (1978) describe *Mesodinium* windrows spaced at 100 m intervals under 10–20 knot winds, and their dispersion through the water column at winds over 30 knots.

Patterning of zooplankton in Langmuir circulations is less apparent and notoriously difficult to sample. The best examples of Langmuir patterning of zooplankton thus are from lakes, where populations of cladocerans and copepods migrate vertically into Langmuir vortices in the epilimnion and form rows of higher concentration in convergence planes (George and Edwards, 1973).

INTERNAL WAVE PATTERNS

Internal waves generate banded patterns on the sea surface on a range of scales extending from that of the Langmuir circulation. Visible rows spaced 10–100 m apart are common on continental shelves, particularly when insolation produces a thin, light surface layer. Ewing (1950) first identified internal waves as responsible for light-wind band slicks and presented evidence that slicks progressed with and marked convergent displacements on the surface layer, moving at 1–100 cm s^{-1}. They are made visible from collection of surface films in compression zones (Garrett, 1967) or directly from the effect of billow currents of internal waves (Gargett and Hughes, 1972), either of which locally damps surface capillary waves. Rows may extend for several km and lie usually more or less parallel to shore, to isobaths and to one another. Row orientation is independent of wind direction, but rows are erased (or replaced by the Langmuir circulation) when wind speed increases about 3 m s^{-1} for 30 minutes or more.

Internal waves on the continental shelf are generated remotely by a variety of mechanisms and altered by changes in density stratification, currents and current shear, and proximity to the sea surface and bottom (see review by Garrett and Munk, 1979). Wind storms and tides are the likeliest common source of their generation. Unlike circulations discussed here, there is no net transfer of water or organisms with the passage of internal waves unless they break. Thus there is no actual circulation of substances and organisms are not differentially collected, except perhaps ephemerally at the very surface. Bacteria depending on the surface film for support are sometimes highly concentrated in internal wave slicks, but more often show no particular relation to them (ZoBell, 1946).

Internal waves, however, may interact with current boundaries and shelf-break fronts. Curtin and Mooers (1975) presented measurements that indicated generation of large amplitude, high frequency internal waves by breakdown of the semidiurnal internal tide at the shelf-break front off Oregon. These induced major perturbation of a sonic scattering layer of organisms inshore of the front. Earlier, Yasui (1961) presented a theoretical framework arguing for generation and propagation of tidal period internal waves along fronts due to current confluence, which are zones of high lateral shear as well as vertical circulation. Localised interaction between internal waves and eddies in mid-ocean also has been detected (Frankignoul, 1976) which may affect rate of vertical diffusion. As yet, these phenomena seem to be unexplored, but may be expected to modify effects of fronts on biota. Kamykowski (1974), for example, presented a reasonable mechanism by which phytoplankton can interact with the semidiurnal internal tide to produce patterns of species and biomass.

Internal waves are sensitive to current shear and to vertical density gradients, both of which are altered at fronts and eddies. It will not be surprising to find evidence of biological responses to these coactive physical processes if adequate sampling techniques can be devised.

4 Coastal fronts and eddies

Topography of the sea floor and obstacles to flow exert locally significant control of convergence systems above the scale of the Langmuir phenomenon and spawn eddies large enough to affect biological processes.

TIDAL FRONTS

Simpson and Pingree (1978), Pingree *et al.* (1977) and Pingree *et al.* (1974) described cases of genesis and maintenance of shallow sea fronts by tidal mixing on the European continental shelf. Surface convergent fronts of considerable physical and biological activity occur in zones where water types of different mixing histories impinge. Where tidally-mixed water contacts stratified water, a convergent front occurs. Thermal images of the Celtic Sea from the NOAA-5 satellite confirm the broad occurrence of tidal fronts and show the genesis of cold eddies from frontal meanders (Fig. 2). These fronts respond to the neap and spring tidal cycle and its effect on phytoplankton chlorophyll concentrations in the stratified water beyond the front. The quoted studies suggest that blooms of a somewhat distant dinoflagellate population were caused by periodic release of nutrients from the destratified side of the front.

Admixture of water types at shelf fronts locally stimulates phytoplankton photosynthesis and thus sustains higher phytoplankton concentrations in the frontal zones. Savidge (1976) and Savidge and Foster (1978) described such a process from surface measurements of chlorophyll, temperature and photosynthesis along transects on the European shelf between Ireland and Wales.

Zooplankton concentrated in shelf fronts is also observed. Pingree *et al.*

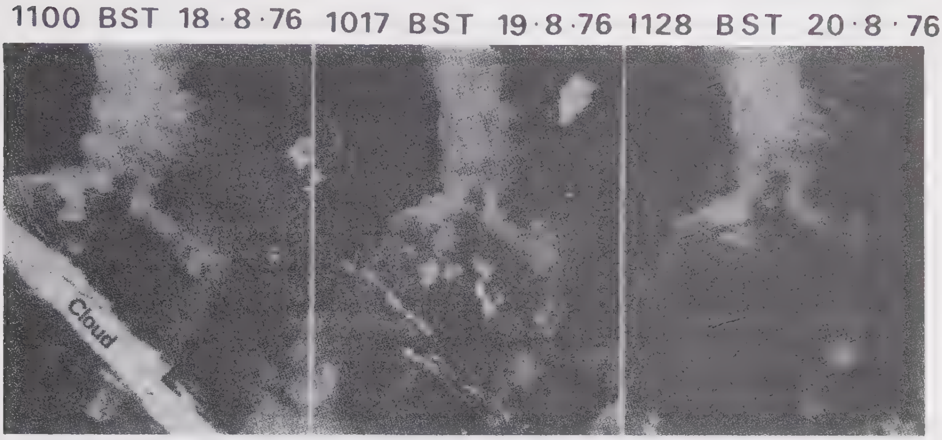

FIG. 2 Infrared images from NOAA-5 satellite of thermal patterns in the Celtic Sea from 18 to 20 August 1976. Lighter shades represent cooler surfaces. From Simpson and Pingree (1978)

(1974) described a vigorous tidal front of 15 km extent in the English Channel from temperature, salinity and current measurements and from direct underwater and surface observations of its effects on organisms and substances. Surface net hauls showed much greater frontal concentrations of copepods, crustacean meroplankton, the euphausiid *Nyctiphanes* sp. and (perhaps) young fishes.

Plankton concentrated by the front was confirmed by subsurface visual observation. Underwater observation of motions of plankton and of dye injected at several depths also confirmed the turbulent and convergent character of the fronts that was apparent from temperature and salinity structure and from drogue measurements. The list provided of animals associated with floating macrophytes concentrated at the front consisted of a variety of post-larval fishes and crustacean species. Puffins, shearwaters and terns were seen feeding along the front, which also collected debris and oil lumps. The authors remark on the similarity of this front and its biota to the large, deep-ocean fronts described by Beebe (1926) and Amos *et al.* (1972).

Marine mammals are documented to exploit the biota of tidal and other shelf fronts. Gaskin (1976), for example, cited feeding by minke whales on herring or capelin aggregated in coastal tide slicks of eastern Canada and feeding by fin whales on surface concentrations of the euphausiid *Meganyctiphanes* in a convergence in the Bay of Fundy. Mackerel schools had forced the euphausiids to the surface.

SHELF-BREAK AND UPWELLING FRONTS

Fronts of large extent commonly occur in the general vicinity of the shelf-break, i.e. where the gradient of the continental shelf steepens to become the continental slope, generally at about 100–300 m depth. Mooers *et al.* (1978) usefully distinguished between prograde fronts, those that separate more saline shelf water from offshore water, and retrograde fronts, those that separate less saline shelf water from offshore water (Fig. 3). Shelf waters of both types usually are colder than offshore.

Prograde fronts arise by upwelling on the continental shelf. Seasonal and episodic wind-driven upwelling is characteristic of eastern boundary current systems, but occurs inshore of western boundary currents as well, where upwelling occurs by topographic deflection or trapping of currents. Retrograde fronts are due to shelf-water dilution from terrestrial runoff and thus predominate off large coastal watersheds. Their incidence and intensity usually vary with season.

Prograde shelf-break fronts off upwelling zones bound plankton rich shelf waters. There is a dearth of studies that demonstrate higher plankton concentrations in these fronts than inshore, at least in part because field studies have been concerned more with the upwelling system as a whole and do not sufficiently sample the frontal interface. Packard *et al.* (1978) described the incidence and habitat of the pigmented ciliate, *Mesodinium rubrum*, in an upwelling zone off Baja, California. Characteristics of its environment in combination with its phototaxic behavior, rapid reproduction rate and ability to use both inorganics and organics for food, were cited to potentiate surface-layer concentrations of the ciliate at prograde fronts.

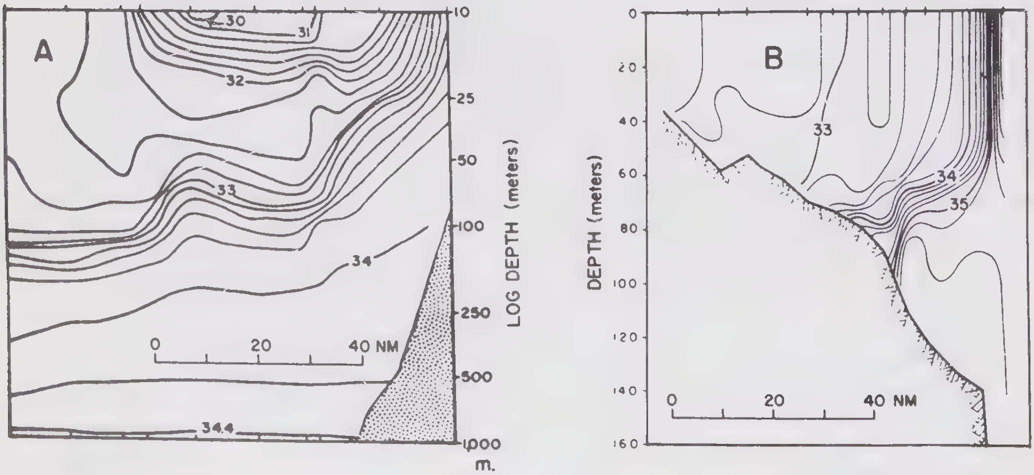

FIG. 3 Structure of prograde (upwelling) fronts and retrograde (estuarine) fronts. Panel A from Owen (1968). Panel B from Mooers *et al.* (1978)

Bang (1973) described measurements showing a strong upwelling front extended northwest off Cape Town in the eastern boundary current of South Africa. Mixing cells occurred and episodic overturn at the front produced subthermocline sheets of homogeneous water. Concentrations of large zooplankton or micronekton were detected at the front by fathometer. The area inshore of this front has begun to support a fishery on the lantern fish *Lampanyctodes hectoris* incidental to the extant anchovy and pilchard fishery of the region (Ahlstrom *et al.*, 1976).

Albacore make annual trans-Pacific migrations to feed on relatively high concentrations of large plankton and small fishes in the California current, seaward of coastal upwelling zones. The offshore extent of these upwelling zones are frequently denoted by prograde (upwelling) fronts. Albacore caught, tagged with ultrasonic transmitters and released were tracked in the vicinity of such a front off Monterey Bay, California (Laurs *et al.*, 1977). Their results showed that such temperature fronts influence local concentration of albacore, with albacore concentrating in the vicinity of the front, moving away with the degradation of the front as upwelling ceased. Albacore also were seen to move more slowly when crossing fronts and to spend little time on the colder side ($t < 15°$ C) indicating a thermal barrier effect which would result in their collecting at fronts. The enriching effects of large cyclonic eddies that predominate outside upwelling zones, and eddy transport from upwelling zones described by Owen (1980) may also support higher forage levels beyond such fronts.

An important aspect of upwelling fronts is their periodic relaxation or breaching, and the subsequent release into offshore water of nutrients and plankton previously accumulated in the shelf water. Frontal relaxation occurs upon cessation of upwelling, which can be either seasonal or episodic depending on the wind system. Breaching occurs more locally than does relaxation. The causes of breaching have not been defined but likely involve meanders and eddies due to local instabilities of frontal currents, outside eddy impingement, and perhaps wave interactions with the fronts. When clear weather permits, breaching is clearly evident in thermal images of sea surface temperature fields off California transmitted from satellites. Bernstein *et al.* (1977) demonstrated the possibility of using such infrared images to follow the genesis, lysis and incidence of eddies, fronts and upwelling zones where they involve temperature, as in the California current system.

ESTUARINE FRONTS

Retrograde (estuarine) fronts exhibit salinity gradients, since freshwater sources dilute surface waters on one side of such fronts. Iisuka and Arie (1969) showed concentrations of *Trichodesmium* (flagellate) for 80 km along an estuarine front off Japan. LeFèvre and Grall (1970) showed similar convergent aggregations of *Noctiluca scintillans* off Brittany, and emphasised local competition for diatoms between *Noctiluca* and copepods.

Owen (1968) studied effects of the Columbia River plume, which albacore encounter in their early summer arrival off Oregon. Based on research vessel catch rates and oceanographic data, results showed that albacore moved through the pronounced outer plume boundary, defined by the 32.2‰ isohaline that demarcated the outer estuarine boundary of the salinity front of the plume-sea interface. Catches were usually lower in mid-plume than in the vicinity of its frontal limits, indicating an attraction to the fronts *per se* or possibly a combined attraction/aversion to the warmer temperatures/lower salinities of the plume core. Catch rates may be seen to be much higher near the outer plume limit than near the inshore limit, where even stronger thermohaline fronts result from combined effects of the plume and coastal upwelling (cf. Fig. 3, panel A).

On smaller scales near shore, Tsujita (1957) showed seasonal onshore/offshore movements of stocks of the Japanese sardine off western Japan. Spawning and hatching occurs at depth in oceanic water near a retrograde (estuarine) coastal front. Larvae are transported or migrate through the shelf-break front and seek nearshore feeding grounds, growing to 7–10 cm and diffusing seaward in summer in the upper layer of the coastal zone.

A large saline front found spanning the Equator 600 km off Sumatra and south of the Bay of Bengal by Amos *et al*. (1972) was formed at the confluence of the saline Equatorial Countercurrent with water from the north, diluted by effluent of the Ganges, Irrawaddy and Salween rivers. Hardly a shelf-break feature, the front still was of estuarine character and exhibited high biological activity: obviously associated with the front were small sharks and flying fish, and feeding sea birds. The front also collected a large quantity of debris and abundant plankton. Sea snakes and dolphin fish also were seen at the convergence. Under no immediate topographic control, the front was nevertheless of estuarine origin.

5 Deep-sea fronts and eddies

Beyond immediate topographic control, confluenced waters of different mixing histories produce a front or frontal system in the equatorial Pacific (Wyrtki, 1966). Pak and Zaneveld (1974) demonstrated increased particle concentrations associated with a front east of the Galapagos Islands (downstream with respect to the equatorial undercurrent) that was defined by large horizontal gradients of temperature, salinity, density and nitrate concentration. They attributed the front to the confluence of the Peru current with the south equatorial current, and cite earlier physical oceanographic investigations of the same feature that indicate its permanence and the seasonality of its location and intensity. It seems possible that this is the same front described by Beebe (1926) that dramatically assembled a large fauna.

Cromwell and Reid (1956) described such fronts (or the same front) from close-spaced temperature profiles along 120 W and 172°W and suggested cell-like circulation from their data (see Fig. 1). Knauss (1957) described a second front crossing at 120°W with even closer temperature profiles that defined the frontal edge. Knauss mentioned high concentrations at the front of squid, *Pyrosoma*, flying fish (2 species), sauries and lantern fish (2 species), and the absence of floating debris. Water characteristics on the cold sides of these fronts indicated the involvement of the east-flowing equatorial undercurrent in their creation and maintenance.

Murphy and Shomura (1972) documented increased availability of yellowfin tuna near island groups of the central Pacific, particularly of younger fish in surface schools. Three assessment methods, sightings of surface schools, surface trolling and deep longlining clearly indicated their increased abundance within 100 km of islands. Concentration of tuna forage by topographic fronts and eddies was suggested to account for the effect.

Murphy and Shomura (1972) pointed out 'the very existence of schools of carnivores would seem to require schools or aggregations of prey, for if prey were distributed at random, it could be most effectively harvested . . . by individual predators'. They showed a close correspondence between the incidence of thermal fronts and tuna school sightings on transects from 10 N to 5 S in the central Pacific beyond influence of islands. They concluded that concentrating mechanisms were more important than overall levels of forage in determining incidence of surface schools, but that the overall forage levels were of more influence on distribution of the much less aggregated deep-swimming tunas.

At higher latitudes, front-prone zones correspond with transition zones of the atmosphere between the easterly tradewinds and westerlies. The region between 22°N and 32 N in the Atlantic appears particularly active in late winter and spring (Voorhis and Hersey, 1964). Voorhis (1969) described shipboard physical measurements of a large, meandering thermal front extending east-west for nearly 1000 km at 27–30 N in the Sargasso Sea. A similar front was later found to persist for 3 months by repeated surface temperature surveys from low-flying aircraft equipped with an infrared detector.

Biological sampling across the Sargasso Sea at other times has shown north-south discontinuities at the front of small particles (Spilhaus, 1968), phytoplankton production (Ryther and Menzel, 1960), species composition and standing stock of phytoplankton (Hulbert, 1964), zooplankton (Colton *et al.*, 1975) and mesopelagic fishes (Backus *et al.*, 1969).

In the Pacific, the annual feeding migration pattern of albacore tuna from waters off Japan to the American west coast appears to be bounded by fronts defining the northern and southern limits of the transition zone separating Pacific central and subarctic water masses. Shomura and Otsu (1956) and Graham (1957) found that mid-Pacific albacore catches were characteristically associated with the subarctic front and transition zone. This zone is probably a consistent source of surface layer enrichment (McGary and Stroup, 1956) indicated by elevated phosphate levels and reduced water transparency due to plankton production. Laurs and Lynn (1977) studied albacore catch rates in relation to transition zone fronts, both under intensive coverage as the fish approached the west coast feeding grounds in late spring. Large catch rates did not persist in any one area for more than a few days, indicating movement of the schools; their degree of constraint between oceanographically-defined frontal zones is apparent in Fig. 4.

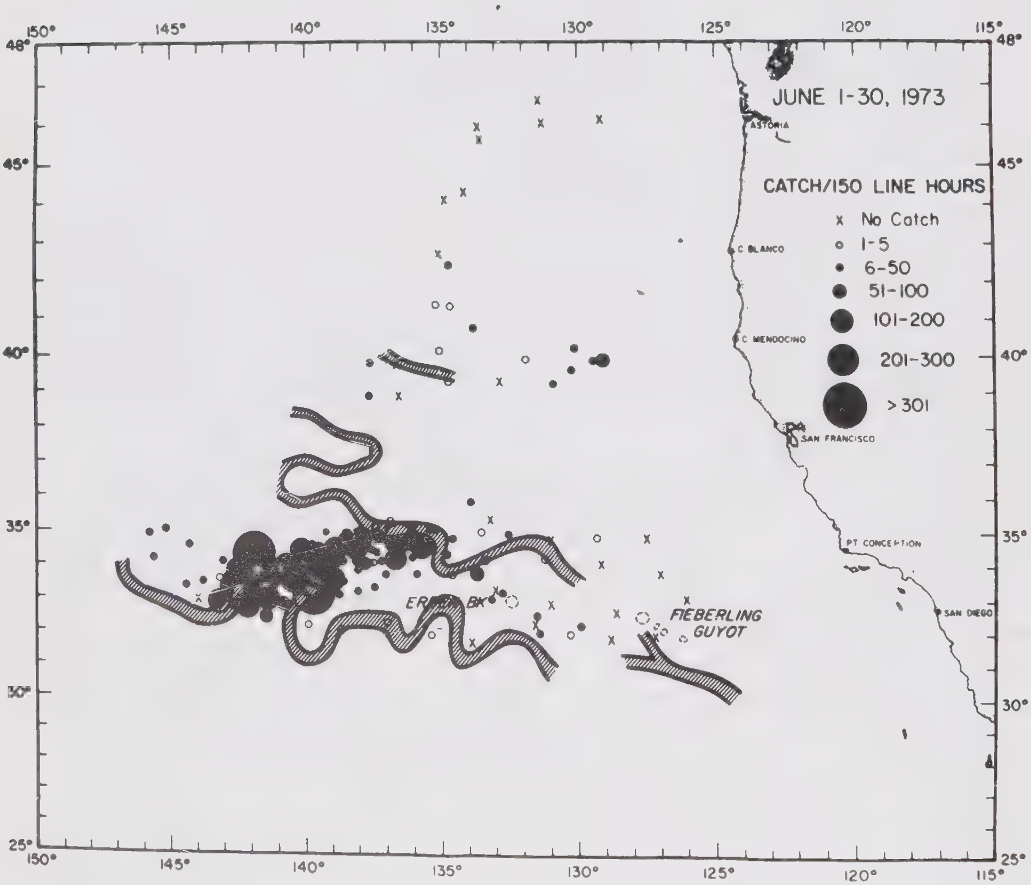

FIG. 4 Albacore tuna catch rate in relation to fronts (shaded) of the transition zone in June 1973. From Laurs and Lynn (1977)

Although not clear from the limited direct measurements available, this transition zone and its fronts probably furnish more food to migrators than waters beyond. Albacore have a fondness for saury and squid, which have been noted to concentrate at frontal structures elsewhere (Uda, 1938, 1952; Han and Gong, 1970). The subtlety of temperature and salinity gradients that define transition zone fronts make it seem unlikely that albacore respond directly to these gradients to determine their movements, although Neill *et al.* (1976) suggested a mechanism by which tunas may orient to temperature gradients as small as 0.1° km^{-1}.

Seckel (1972) suggested that convergent flow along the large-scale saline front between North Pacific central and equatorial water masses may operate directly to concentrate skipjack tunas as well as their food. This front is demarcated by a horizontal salinity gradient that periodically reaches or passes the Hawaiian Islands; the abundance of skipjack, indicated by skipjack catch by local fishing, increases at these times. This suggests at least a bounding effect on the fish. The northward passage of the front is detected by the sharp decrease (here, in May) of salinity at a shore station on Oahu.

A growing body of evidence suggests that topographically independent baroclinic instabilities (wavelike motions in large-scale flows with vertical shear in which Coriolis and buoyancy forces are important) are significant in large-scale ocean circulations. Hart (1979) reviewed the theoretical basis of this large eddy-producing phenomenon and Hide and Mason (1975) reviewed annulus convection experiments in laboratory flows. In addition to the meanders and eddies of the Gulf Stream and Polar Front cited below, examples of such activity are apparent in the central North Pacific. Bernstein and White (1974), from four sets of temperature observations, verified the existence of a mosaic of baroclinic eddies well removed from islands, ocean boundaries and the Kuroshio.

TOPOGRAPHIC CONTROL OF DEEP-SEA EDDIES

It is equally apparent that continental margins dissipate energy through generation of large eddies. Even in the weak and diffused eastern boundary currents, evidence of boundary effects extend well past continental margins (shelf and slope areas). These are evidenced by thermal patterns from satellites (Bernstein *et al.*, 1977) (Fig. 5). Owen (1980) reviewed eddy genesis and incidence in the California current system and demonstrated the preponderance of cyclonicity among large eddies detected in geostrophic flow by extensive surveys of the California Cooperative Oceanic Fisheries Investigations (Wyllie, 1966). One particularly persistent feature is the southern California Eddy which appears to collect and recirculate biota from the upwelling zone north of Pt. Conception. Owen (1980) indicated

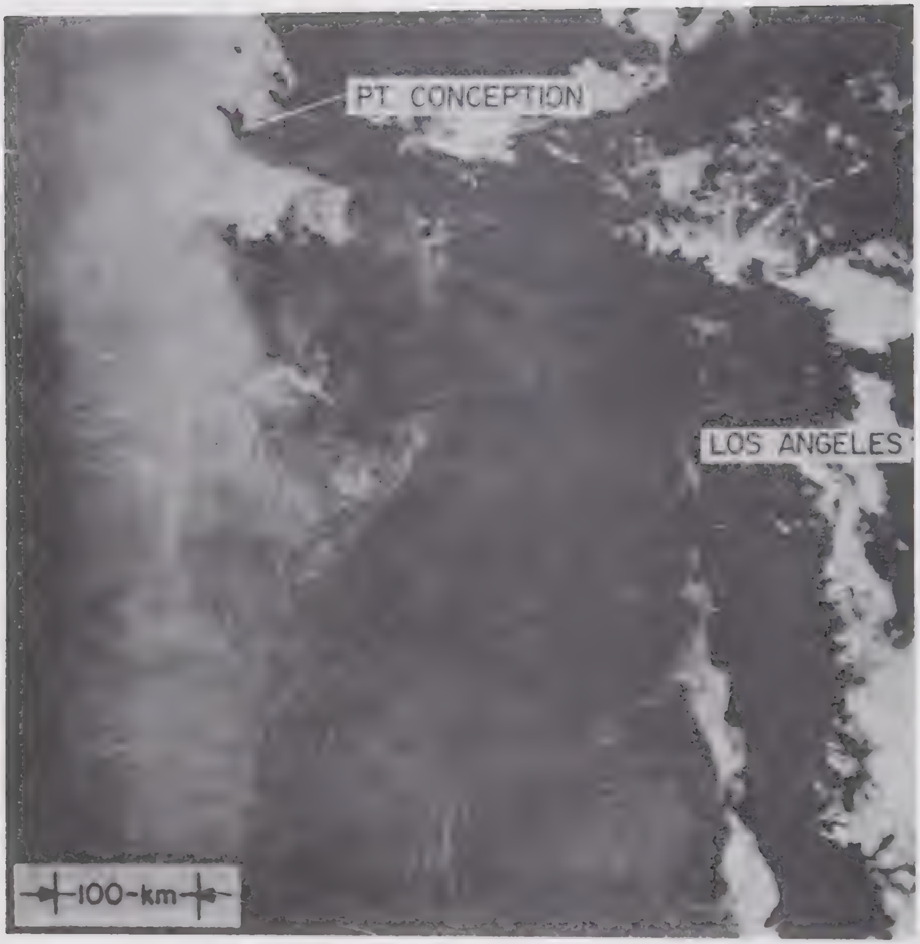

FIG. 5 Infrared image from NOAA-6 satellite of thermal patterns in the southern California Bight, September 1979. Point Conception and the Channel Islands are visible in the upper left quadrant. Lighter shades represent cooler surfaces. Photo courtesy of Remote Sensing Facility, Scripps Institution of Oceanography

the role of the Eddy in nutrient enrichment of the surface layer by upward flow and nutricline displacement. Washdown of diatom assemblages was indicated by Allen (1945) and higher chlorophyll concentrations in the Eddy were shown by Owen (1980). Brinton (1976) examined life history and local distribution of *Euphausia pacifica* which suggested the Eddy to be a reproductive refuge for the population. The correspondence is unmistakable between the Eddy and patterns of concentration of both sardine eggs (Sette and Ahlstrom, 1948) and diatom concentrations (Sargent and Walker, 1948) in spring of 1941.

Another large, stationary eddy is even more isolated; the Costa Rica Dome is produced by topographic deflection of the north equatorial countercurrent. The Dome, named for its upward bulging thermocline layer, centers in the bight of this deflection (Fig. 6). Upward displacement and active upwelling in the core region cause nutrient enrichment of the photic zone (Broenkow, 1965). This sustains detectably higher stocks of phytoplankton, zooplankton and small nekton according to authors cited by Owen (1980).

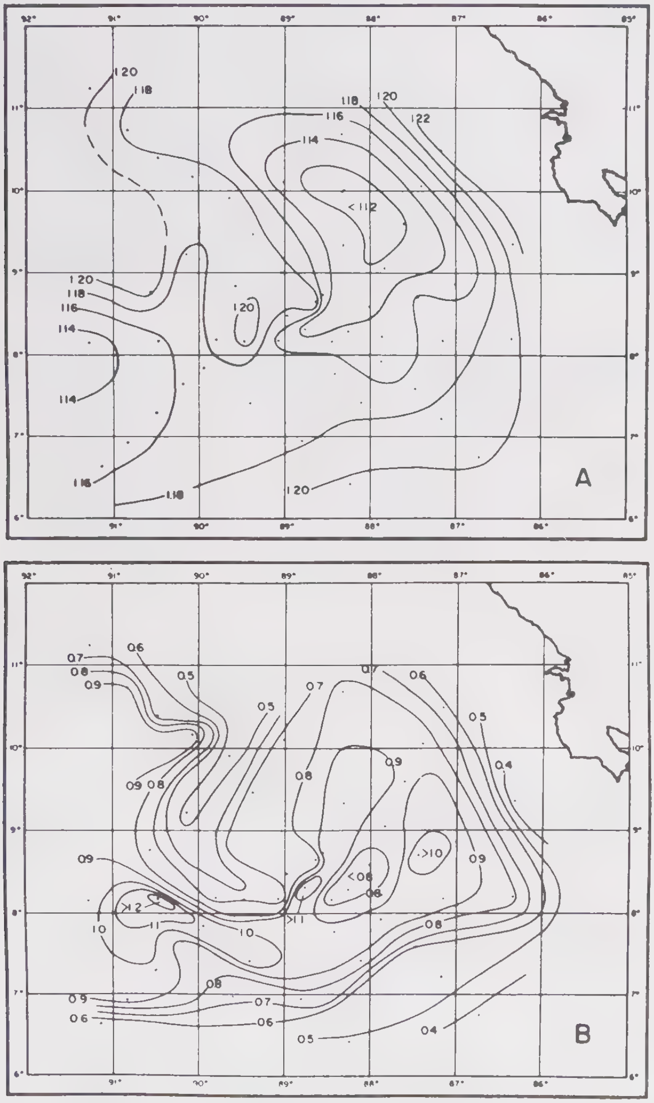

FIG. 6 (A) Flow represented by geopotential topography of the Costa Rica Dome at about 50 m depth relative to 1000 m. (B) Phosphate concentration (μg atoms l^{-1}) at 50 m depth. From Broenkow (1965)

Islands, seamounts and headlands act as obstacles to sea and air flow and induce instabilities that can develop into eddies. Eddies may be stationary, "attached" to the obstacle or, with increased flow or obstacle size, may be shed in series. Barkley (1972) found remarkable agreement between observed current patterns downstream of Johnson Atoll and an adaptation of

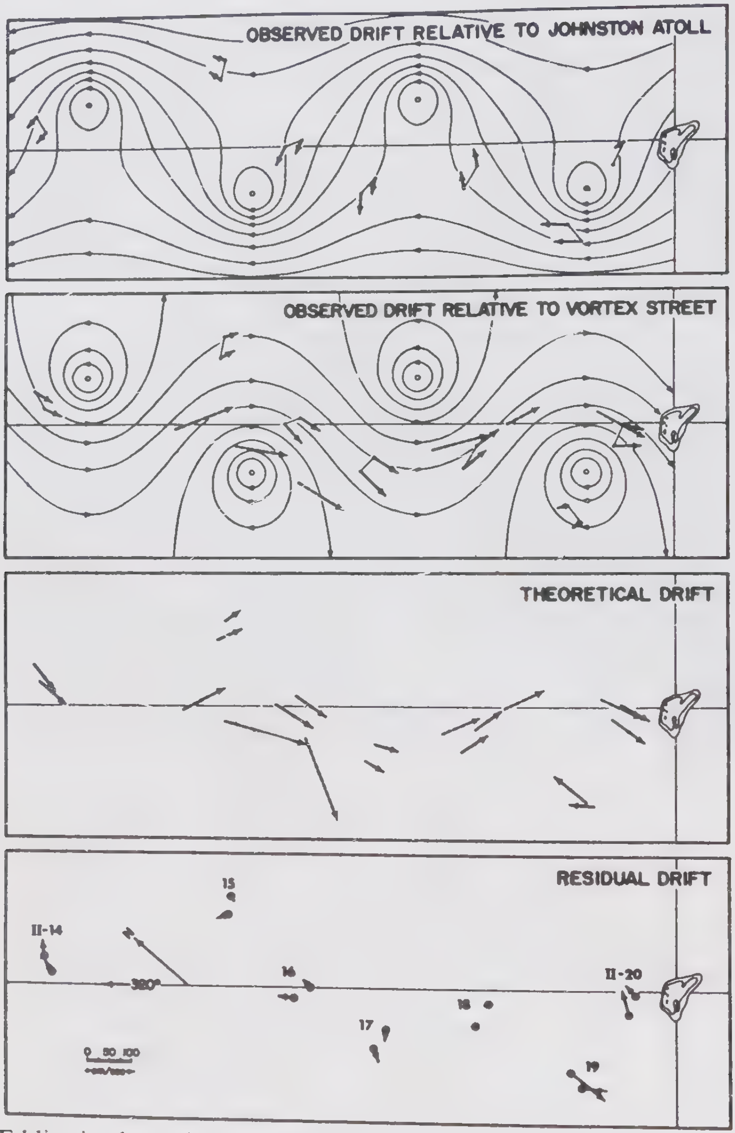

FIG. 7 Eddies in the wake of Johnston Atoll. Streamlines in upper panels derived from von Kármán model of vortex street, fitted to current measurements. Degree of fit is apparent from the lower panels; residual drift values are small compared with theoretical and observed values. From Barkley (1972)

Von Kármán's model of flow past cylinders (Fig. 7). Patzert (1970) described eddy systems in the lee of the Hawaiian group, where eddies appeared to form by local wind forcing. White (1973) detected eddy patterns east of the Galapagos, with respect to the equatorial undercurrent. Wind or current effects at headlands produce eddies, perhaps acting as half an island. Arthur (1965) identified the importance of flow vorticity at headlands of west coastlines. Where the thermocline and nutricline are shallow, the eddy formation produces cool, enriched water at the surface equatorward of such promontories (Reid *et al.*, 1958).

Boden (1952) and Boden and Kampa (1953) determined summer and winter circulation patterns over the submerged platform of the seamount from which Bermuda emerges. Distribution of density in both seasons indicated a cyclonic eddy spanning the entire seamount, and convergent fronts at its margins. The planktonic larvae of benthic animals sampled in summer were considered to be returned to and retained on the platform by both eddy and frontal circulations, enhancing their eventual recruitment to the bottom fauna. Intense mixing zones close to the platform sides were indicated by local vertical instabilities as density inversions.

Hogg *et al.* (1978) detected eddies near the Bermuda Platform (Fig. 8). Fine-structure of temperature variation on intervals from 0.2 to 25 m indicated a large degree of vertical mixing in patches close to the island, a consequence they felt due to strong longshore flow between the eddies. Hogg *et al.* (1978) attribute one of the eddies to a meander in the Polar Front. Intense mixing zones occurred on small scales (0.2–1 m variances) next to the platform walls (note Boden and Kampa's result above) and on larger scales (5–25 m) at about 10 miles distance. Velocity profiles showed that the vertical scales of mixing increased with distance from the island. Internal waves were discounted as a source of the mixing. Osborn (1978), using measurements of velocity shear microvariation, found zones of high energy dissipation (by mixing) within 5 km of the island of Santa Maria in the Azores. Mixing zones were as much as 45 m thick, at the base of the upper mixed layer. At 80 km distance, maximum dissipation zones were below the thermocline at depths over 250 m.

Emery (1972) described evidence from drift bottle and current meter data favoring a persistent system of shed eddies in the wake downstream of Barbados Island (West Indies). Weekly evening plankton tows made 3 km off Barbados for over a year indicated that retention or return of meroplankton near the shelf of the island was enhanced by the eddies.

Jones (1962) cited evidence for effects of the Marquesas Islands in the equatorial Pacific. He found significantly higher zooplankton volumes in quantitative net tows approaching the islands from any direction in the zone from 10 to 180 miles. The higher plankton concentrations were not due to

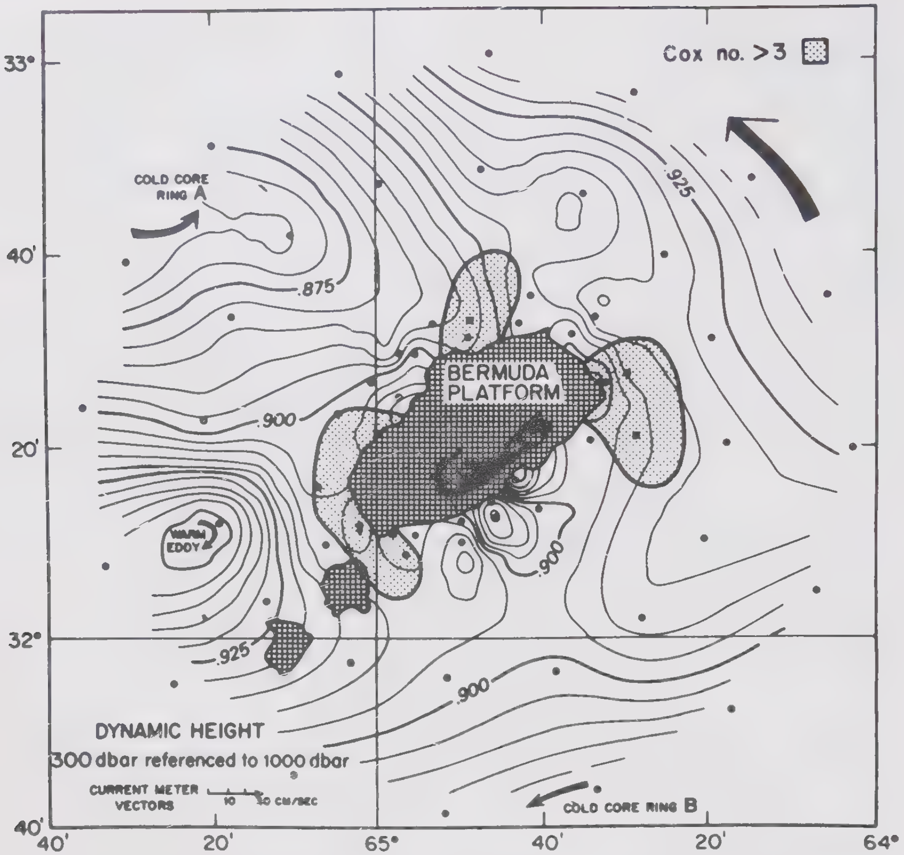

FIG. 8 Flow represented by geopotential topography and intense small-scale mixing zones at about 300 m depth near the Bermuda Platform, according to Hogg *et al.* (1978)

washout of island plankton as most were dominated by euphausiids and siphonophores. Neither group is considered land dependent. The decrease in water transparency approaching the island zone is consistent with higher phytoplankton stocks.

FRONT-EDDY INTERACTIONS

Large-scale associations of fronts and eddies are apparent from several examples. Where fronts are vigorous for their size or meet an obstacle, flow becomes unstable and frontal meanders may pinch off and become eddies as shown in Fig. 9 (Fuglister and Worthington, 1951). Western boundary currents and their seaward extensions produce large intense fronts and eddies. A well-documented example is spawning of eddies from the North

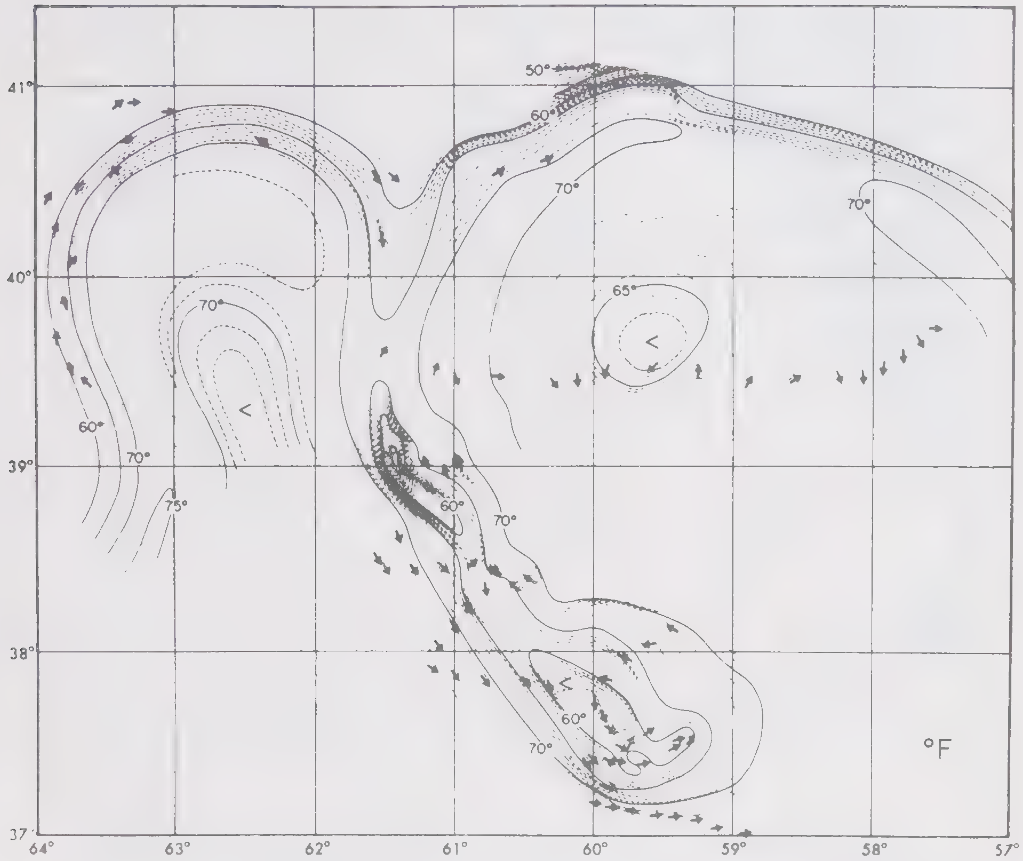

FIG. 9 Cyclonic eddy genesis from a Polar Front meander. Temperature pattern at 200 m depth and measured current vectors (→) delimit a cold core meander and eddy pattern. From Fuglister and Worthington (1951)

Atlantic Polar Front. The front is a product of the seaward extension of the Gulf Stream axis into mid-Atlantic and is defined by the large temperature gradient between cold shelf or subarctic water to the north and warm Sargasso Sea water to the south. Flow instability periodically produces a large meander of the Front that is subsequently shed as an eddy. If shed south or east of the front, the eddy contains colder water from the north side and is cyclonic, whereas warm-core, anticyclonic eddies spin off into colder water to the north and west (Fig. 10). Cyclonic eddies so form several times a year and are physically identifiable for as much as 2 years (Parker, 1971). Initially, they range to 300 km diameter laterally and extend from the sea surface to 3 km in depth. Such eddies do not always extend to the sea surface. Howe and Tait (1967) detected a sub-thermocline eddy generated

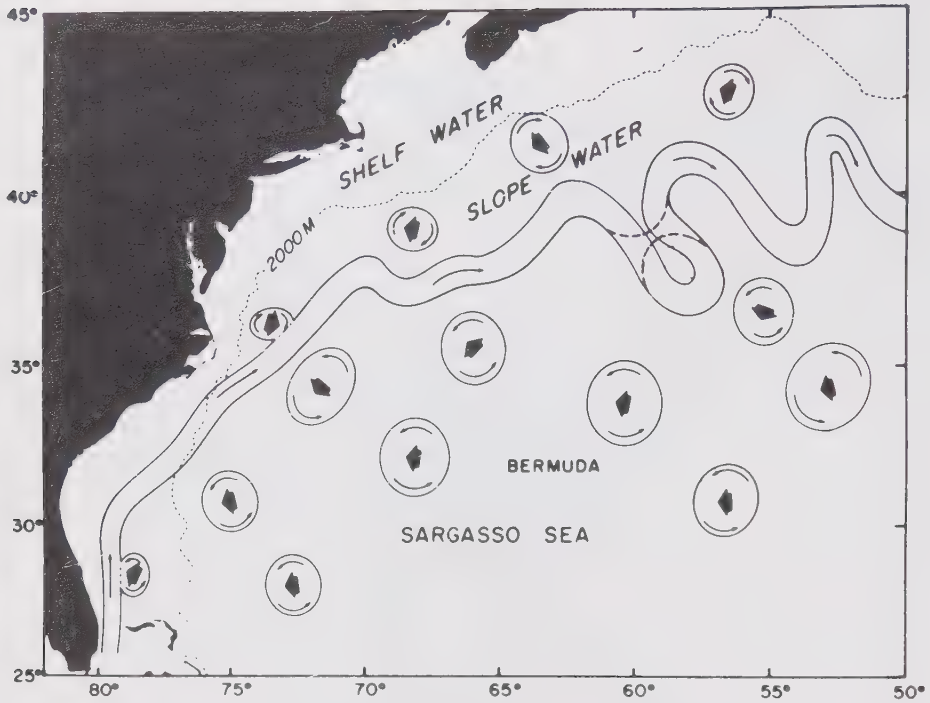

FIG. 10 A schematic representation of the path of the Gulf Stream and the distribution and movement of ring eddies by Richardson (1976)

by a meander of the Polar Front. This eddy centered at about 650 m depth and extended from 150 m to perhaps 1200 m. Circulation strength at the core depth was about 10 cm s^{-1} and the eddy extended laterally about 60 n.mi. Surface layer involvement may have been eradicated by local processes (e.g. wind-induced transport) prior to its detection and measurement. Biological effects peculiar to subsurface eddies are easily imagined but were not assessed.

Predominantly under dynamic control, both the Polar Front and eddy genesis appear to be under local topographic control where the front crosses the mid-Atlantic Ridge. From detailed oceanographic station patterns, Dietrich (1964) noted marked weakening at the Ridge of the temperature and salinity gradients that define the Polar Front at 200 m depth. A major dislocation of the front also occurred at its Ridge crossing: the dislocation took the form of a meander of the type that is a cold-core eddy precursor (Fig. 11, Panel A). Flow direction and speed of the sea surface relative to that at about 1000 m show this meander as well as the blocking or dissipative effect on the Front of the Ridge (weaker gradients of dynamic height east of the Ridge in Fig. 11, right). Topography of the sea floor is elsewhere unlikely to affect the Polar Front and its eddies, once clear of the American continental slope.

Eddies from the Gulf Stream and Polar Front tend to conserve the biomass and community structure of plankton isolated when they form. Noting their potential for biological interaction, Wiebe *et al.* (1976) summarised biological measurements in several cold-core eddies from the Polar Front. Initially containing plankton stocks of cold-side origin, young cold-core eddies exhibited relatively higher plankton biomass and species assemblages that were distinguishable from surrounding Sargasso Sea waters. With increasing age, such eddies attenuate and assume the physical and biological character of the surrounding water, but may be biologically distinguishable for more than a year.

Phytoplankton biomass and species composition differences in the eddies usually attenuated in about 6 months, or less in one case when storm mixing of the phytoplankton habitat occurred. One young eddy may have generated its own phytoplankton assemblage. Phytoplankton composition in this eddy was shown to differ from that of the source waters as well as from that of Sargasso Sea waters.

Zooplankton biomass and species ensembles of cold-core eddies took considerably longer to attenuate. Consistently higher zooplankton stocks and distinctive euphausiid species were evident in eddies as old as a year. Diel migration patterns of several zooplankton species also appear to have been affected by the presence of the eddies. Daytime depths reached by warm-water euphausiid species that migrate was consistently and markedly deeper beyond than within a cold-core meander of the Polar Front.

Weibe and Boyd (1978) later examined distribution limits of one of the cold-water euphausiids, *Nematoscelis megalops*, involved in the Polar Front and eddy complex. The study illustrates a compund front-eddy effect. The Polar Front (like other western boundary currents) is shown to be an effective thermal barrier to some oceanic plankton species, including *Nematoscelis*. Cold-core eddies shed from the front, however, violate the barrier by transporting *Nematoscelis* far south of where they would otherwise occur. Reduced numbers and nutritional condition of individuals in older eddies indicated that expatriate populations attenuate in time by starvation.

Haedrich (1972) reported midwater trawl catches of myctophids and gonostomatid fishes in the Northwest Atlantic. Much reduced numbers of species and fish biomass were noted in catches at a station in a newborn warm-core eddy on the continental slope north of the Polar Front, compared with species diversity and biomass of catches made at four slope and six warm-water stations.

Dynamic generation of large-scale fronts and eddies is not confined to the

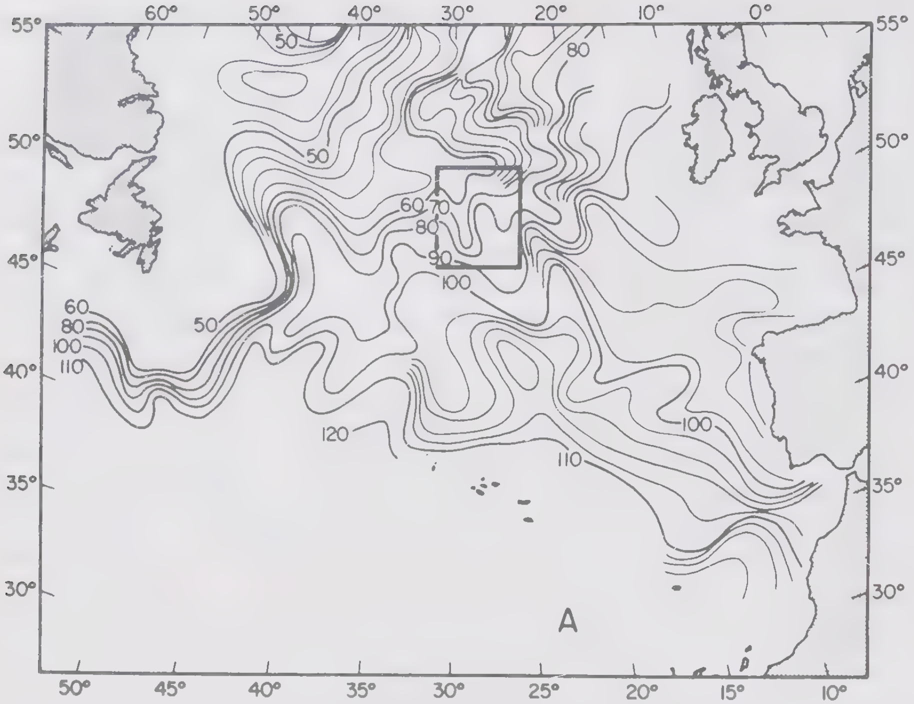

FIG. 11 (A) Flow represented by geopotential topography of the sea surface (relative to that at about 1000 m) in the northern North Atlantic in late summer 1958.

Gulf Stream extension but appears to be characteristic of extensions of other western boundary currents as well. The zone of departure from the South African coast of the Agulhas Current is characterised by complex patterns of vigorous fronts and eddies (Fig. 12). Bang (1970) described the cyclonic eddy 'K' of 50 n.mi. diameter circulating at as much as 6.6 kt at the surface and extending to more than 1600 m depth. Eddy induced vertical displacements of about 500 m were measured in the temperature field. Retroflexion of Agulhas Current water (temp. > 25 °C) is seen from the shaded part of the figure, as this water is redirected eastward by the West Wind Drift. The narrow strip of cold surface water (14–20 °C) above the 'north wall' of the Agulhas Current emphasises the locally divergent nature of what is characterised by Bang as a strongly convergent and eddy-prone frontal system.

Bass (1970) identified the role of the Agulhas retroflexion zone (Agulhas Bank) and the Natal coast as nursery areas for sharks. Four species use Agulhas Bank, 8 other species use the Natal coast. Nursery grounds are on fringes of adult distribution.

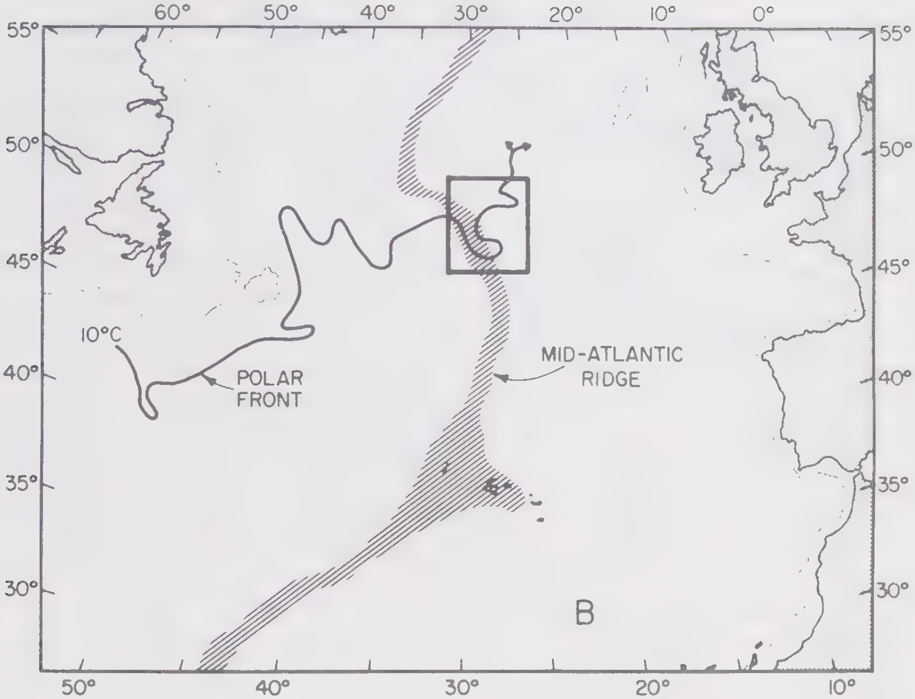

FIG. 11 (B) The oceanic Polar Front axis at 200 m depth in late summer 1958 in relation to the axis of the mid-Atlantic Ridge. Both panels from Dietrich (1964)

Western boundary currents of the Pacific also are well-known to produce fronts and eddies. Strong flow south and flow along the Australian east coast produce large and persistent eddy circulations (e.g. Nilsson *et al.*, 1977). Some of these may be recurrent, or quasi-stationary, suggesting topographic control. Anticyclonic eddies greater than 250 km diameter are particularly common southeast of Sydney. Sufficiently intense biological investigation of the anticyclonic eddies has only recently begun.

The Kuroshio Current off Japan's east coast and its confluence with the south-flowing Oyashio Current are also active generators of large pulsative fronts and eddies. These have long been recognised by Japanese fishermen to attract squids, fishes and mammals (Uda, 1938). Regularity of the eddy patterns along the Oyashio Front, which defines the axis of confluence, led Barkley (1968) to note that these patterns take the form of two vortex streets lying side by side. This mechanism suggests that the Front acts as a perturbing obstacle to the flow of both impinging currents. Because much of the energy of both currents is expended in eddy formation in the confluence region, the Polar and subtropical fronts extending eastward therefore are weaker than the topograpically deflected Gulf Stream.

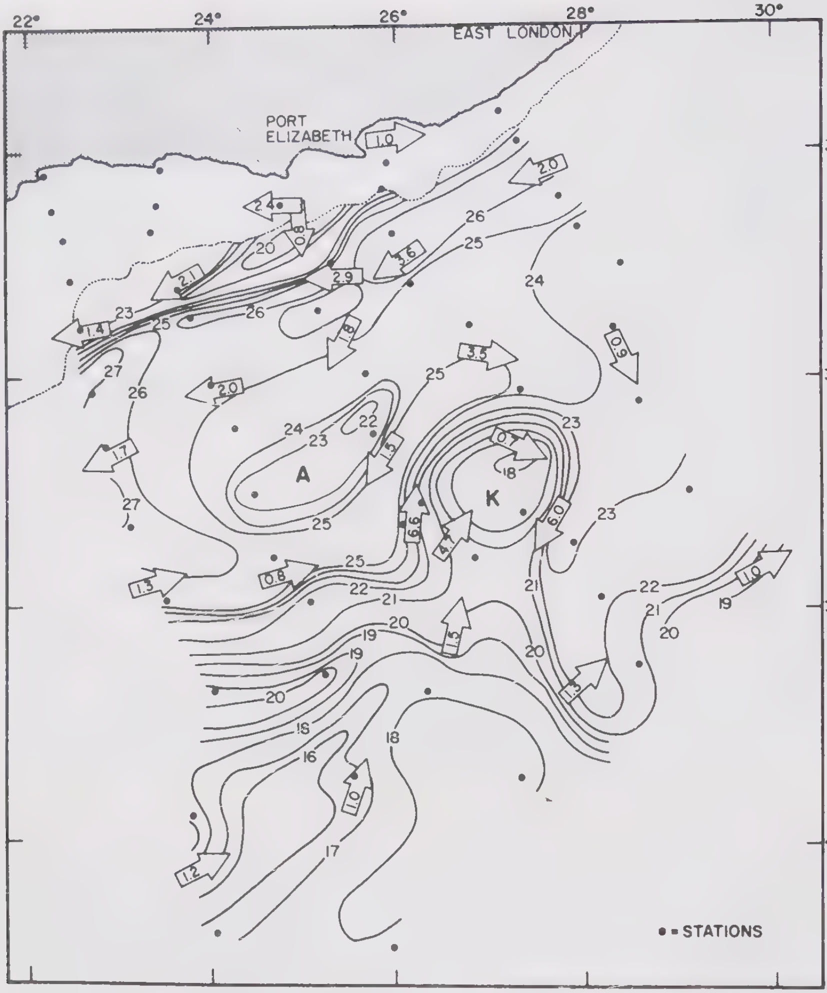

FIG. 12 Surface temperatures, navigation set vectors in knots, and station positions in the Agulhas retroflexion area (southeast tip of Africa) in March 1969. 'A' and 'K' designate adjacent cold-core eddies. From Bang (1970)

Eddy generation also appears to be mediated by flow of air from land masses. Worthington (1972), noting great mixed layer depths and high pressure zones associated with outbreaks of continental polar air over the Pacific south of Japan and over the Atlantic south of New England and east of Newfoundland, believes that convergent sinking of surface water occurs as a result, generating anticyclonic eddies. Anderson *et al.* (1970) consider that flow instabilities of the Agulhas Current off Durban are induced by offshore wind components indicated by local pressure variations.

Since Uda's (1938) comprehensive study of fronts off Japan and their genesis of eddies, the relation of both to the regional Japanese fisheries has received wide attention. Particularly well documented is the effect of the Kurile Front on saury fishing. The Kurile Front is the northernmost of a series of fronts usually found in the Oyashio (Uda, 1938) and is probably analogous to the Polar Front since it forms the southern limit of subarctic water. The most productive saury fishing areas in the northwest Pacific occur in series of eddies along the Kurile Front in summer and fall. This front extends only to 50 m depth. Han and Gong (1970) confirmed this association, showing sensitivity of the saury fishery off the east coast of Korea to the local equivalent of the Polar Front.

Uda (1938, 1952, 1973) and Uda and Ishino (1958) described various associations with fronts and frontal eddies of albacore, yellowfin, skipjack and bluefin tunas, mackerel, salmon, whale species and squid. Feeding, or spawning and feeding provide the biological driving forces for their interaction with fronts and eddies.

6 Summary and conclusion

Combination of physical characteristics of fronts and eddies with interactive characteristics of organisms leads to the following catalog of ecological effects. Many of these have been shown to occur or to account for observed phenomena. Through organisms' sinking, swimming and production, as dictated by food needs and environmental gradients, such quasi-ordered velocity fields have accounted for quasi-ordered patchiness of marine organisms on widely different time and space scales. Fronts and eddies can:

mechanically affect local concentrations of organisms,
juxtapose populations that would not otherwise interact,
create new 'communities',
conserve and translocate selected species ensembles and concentrations,
attract and sustain large motile animals,
serve as reproduction refuges,
mechanically limit dispersal of meroplankton or neritic populations,
selectivity pattern components of populations or communities (quasi-ordered patchiness),
induce/sustain higher local production of organisms,
modify migration patterns as diverse as annual, trans-oceanic fish movements and diel vertical migrations of motile phytoplankton,
collect surface active and particulate substances.

We see that on every scale of frontal and eddy activity in the open sea, there are examples of ecologically significant effects operating through food web stability, community structure, local population dynamics, phytoplankton production and standing stocks, etc. This creates the increasingly distinct view that life forms tend to tesselate the environment in horizontal patterns that are partly governed by vertical exchange due to a variety of physical processes. The scale of the phenomenon and its ecological effect depend on the type and scale of the driving mechanisms, but the resulting biological pattern is also controlled by the organism, its own physical characteristics, behavior, food requirements and response to environmental change.

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Transport Mechanisms and Reproductive Success of Fishes in the California Current

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Abstract Surface marine observations are used to infer the large-scale seasonal patterns of ocean surface drift near the coast in the California Current. Reproductive strategies of the most successful coastal fishery species show a pattern of correspondence to the major features of surface transport. In the Pacific Northwest, coastal fish species having pelagic larvae tend to spawn during winter when surface wind drift is generally directed toward the coast, rather than during the more productive upwelling season. In the region of vigorous upwelling off northern California, which is characterized by strong offshore surface transport through most of the year, there is a paucity of locally spawning species with epipelagic eggs. The fishes spawning in this region have a wide range of reproductive strategies that reduce the planktonic phase of the early life history. Local coastal stocks comprise a minority of the fish biomass in the region. Rather, the fish stocks that harvest the massive productivity of this region are primarily migrating species that spawn under the more favorable drift

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conditions in the Southern California Bight. Closed gyral circulations in the Southern California Bight and off southern Baja California appear to foster favorable spawning conditions that have led to distinct subpopulations of pelagic fishes.

The apparent dependence of spawning strategies upon surface drift conditions suggests the hypothesis that anomalies in surface drift patterns could be a major cause of the observed wide variations in spawning success of the major fishery species of the California Current region.

Egg and larval transport is a critical process in the life cycle of many marine organisms. Typically, spawning grounds are ‘‘upstream’’ in relation to ocean current flow from nursery grounds. The reproductive strategies of many marine species are adapted to fit the prevailing currents, which are relied upon to bring the largely planktonic larvae to nursery grounds usually found in relatively shallow or inshore waters. In order for survival to be adequate, there must be sufficient food during the larval drift period, and the currents must allow the larvae to arrive at the nursery grounds at the proper time and size (Stevenson, 1962; Parrish and Saville, 1965; Ketchen and Forester, 1966; Cushing, 1967). The potential inshore nursery grounds are limited in the California Current region due to the narrow continental shelf. In addition, during certain seasons the prevailing winds cause seaward drift of surface waters, favoring offshore dispersion and loss of larvae. The segment of coastline from Cape Blanco to Point Conception, in particular, is characterized by minimal shelf area and is subject to intense offshore surface drift through much of the year.

The fish fauna of the California Current region is composed principally of elements of a cold-temperate fauna centered in the Pacific Northwest (i.e., the area north of Cape Blanco) and a subtropical fauna centered in the southern California–Baja California region. The transition region between Cape Blanco and Point Conception contains elements of both faunas. Two other faunal groups are well represented in the California Current region: an offshore assemblage (central water mass forms) and a component of the eastern Pacific tropical fauna, which extends into southern Baja California. Many of the hypotheses discussed here probably do not apply to the offshore and tropical faunas.

The exploitable fish biomass in the California Current System is dominated by a small number of pelagic species (Table 1). The spawning grounds of these stocks are primarily in areas characterized by weak coastal upwelling. These fishes, or very closely related species, dominate the fisheries of the three other major eastern boundary current systems (Bakun and Parrish, 1980). Ryther (1969) pointed out that the fisheries of upwelling regions are dominated by pelagic fishes that have relatively short food chains, whereas the fisheries of higher latitudes are dominated by demersal fishes with somewhat longer food chains. The

Table 1.
Peak landings and biomass estimates
(in thousands of metric tons)
of the dominant exploitable fishes spawning
in the California Current region.

Species	*Peak Landings by Region*				*Biomass Estimates*	
	Total	*Pacific Northwest*	*Region of Maximum Upwelling*	*Southern California Bight*	*Peak Year*	*Recent*
Sardine	718[a]	91[a]	529[a]	167[a]	3625[a]	5[b]
Anchovy	288[c]	—	21[d]	284[c]	7067[e]	NA
Hake	231[f]	161[g]	101[g]	—	3270[h]	1519[g]
Jack Mackerel	68[i]	4[g]	15[j]	66[d]	1905[k]*	NA
Pacific Mackerel	66[l]	—	2[l]	64[l]	438[m]	167[n]
Pacific Ocean Perch	39[o]	39[o]	—	—	120[f]	18[f]
Rockfish (other)	33[f]	18[f]	11[f]	5[f]	NA	NA
Sablefish	17[f]	7[f]	6[f]	4[f]	NA	61[f]
Dover Sole	16[f]	7[f]	10[f]	—	NA	NA
Bonito	16[p]	—	—	16[p]	NA	NA
Saury	—	—	—	—	266[q]*	NA
Shortbelly Rockfish	—	—	—	—	295[f]*	295[f]*

*—minimum estimate
NA—estimates not available

[a] Murphy (1966)
[b] Klingbeil (1974)
[c] Preliminary 1980 Mexican and California catch[1]
[d] California Marine Fisheries Branch (1954)
[e] Vrooman and Smith (1971)
[f] Pacific Fisheries Management Council (1980)
[g] Dark (pers. comm.[2]/
[h] Alverson and Larkins (1969)
[i] Knaggs (1979)
[j] California Bureau of Marine Fisheries (1952)
[k] Blunt (1969)
[l] California Bureau of Commercial Fisheries (1937)
[m] Parrish and MacCall (1978)
[n] Klingbeil (1981)
[o] Gunderson (1977)
[p] Collins et al. (1980)
[q] Smith et al. (1970

California Current System is no exception. Pelagic fishes dominate in the southern part of the system where upwelling occurs throughout the year. The northern portion of the system, where upwelling is highly seasonal, has had extensive demersal fisheries in addition to pelagic fisheries.

The purposes of this paper are (1) to present a simplified, but unified and consistent, description of broad time and space scale characteristics of ocean surface flow in the California Current region, and (2) to point out a gross pattern of correspondence to these features among the reproductive strategies of the most successful coastal fish stocks. We believe that this correspondence offers useful insights into the factors regulating recruitment and exposes fruitful directions for further research.

Transport Mechanisms

Seasonal Flow Patterns

The two components of near surface ocean flow that are fundamental to our hypotheses are the surface wind drift, which is the water being carried along in the ocean surface layer under the direct action of the wind, and the underlying geostrophic current field. The geostrophic flow is associated with pressure gradients in the ocean. Its contribution to the near surface velocity field can be inferred largely from temperature and salinity structure. Present understanding of surface wind drift is based on Ekman's (1905) theory, in which the total transport (Ekman transport) in the wind-drifted layer is completely determined by the intensity of the wind stress on the sea surface. On the rather large time and space scales involved in the larval drift problem, transport in the surface layers of the ocean may be adequately viewed as a simple linear combination (i.e., vector addition) of contributions due to these two flow components. The conceptual picture is of a thin surface layer of Ekman wind drift that varies in phase with large-scale atmospheric weather patterns superimposed on a deeper, more slowly varying geostrophic flow field. The physical basis for this conceptual model comes from scale analysis of the terms in the hydrodynamic equations (Greenspan, 1968).

Geostrophic Current

The annual mean geostrophic flow at the sea surface (Figure 1A) was constructed from temperature and salinity summaries produced by Robinson and Bauer (1973), who pooled the available observations within areas defined by 1° increments of latitude and longitude to yield long-term annual mean values at standard depths. Dynamic topographies relative to the 1,000 db level (1,000 m) were computed following La Fond (1951), and a velocity vector for each 1° square was calculated from the gradients defined by dynamic height values in the directly adjacent 1° squares. The result is a rather smooth field in which much of the temporal and spatial detail available in finer scale summaries (Wyllie, 1966) has been filtered out, revealing the large-scale features that provide the basis for our arguments.

The nearshore surface geostrophic flow tends to parallel the coast and, south of Cape Blanco, to be directed equatorward. The general direction of geostrophic flow into the Southern California Bight and toward the coast south of Point Conception is significant to our argument. This is a consistent feature during all seasons, being evident in all of Wyllie's (1966) long-term monthly charts. However, seasonal alongshore surface current features, such as the Davidson Current (Sverdrup et al., 1942), are suppressed in Figure 1.

The pattern of geostrophic flow at 60 m (Figure 1B), constructed by analogous procedures, is similar to that at the surface, but shows a tendency for less southward (more northward) flow near the coast. Thus, the area within 200 km of the coast is characterized by greater vertical shear in the velocity structure in the upper layers of the ocean. This northward tendency in the near coastal subsurface flow relative to the flow at the sea surface is associated with the California Undercurrent (Reid, 1962, 1963; Wooster and Jones, 1970) and continental shelf poleward undercurrent (Smith, 1974; Pedlosky, 1974) phenomena.

Surface Wind Drift

Quarterly distributions of Ekman transport (Figure 2) were computed from Nelson's (1977) stress summaries. Ekman transport is calculated as the ratio of the wind stress magnitude to the local value of the Coriolis parameter and is directed 90° to the right of the wind stress (in the

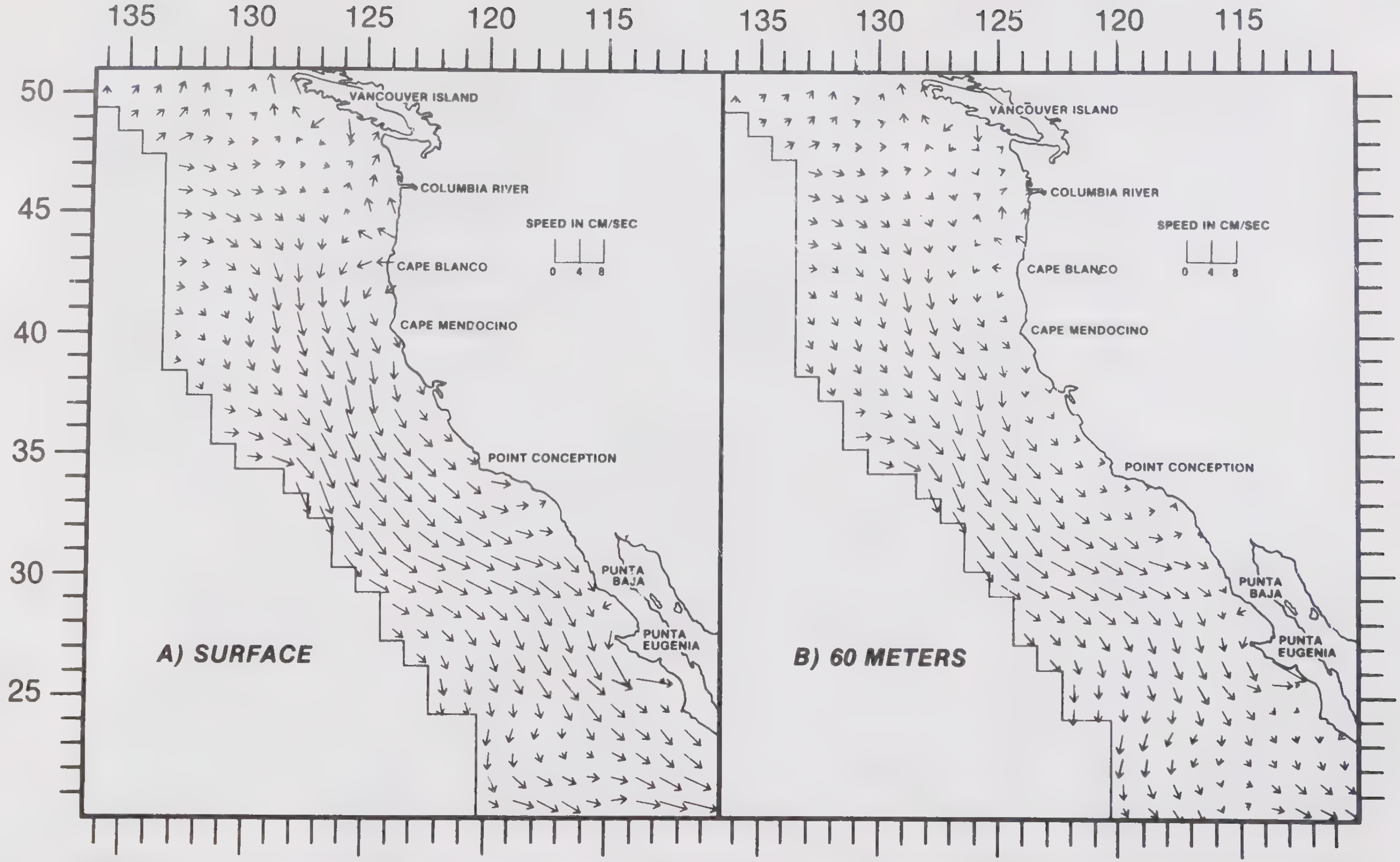

FIGURE 1. Mean geostrophic flow: A. at the sea surface (0/1000 db), B. at 60 m (60/1000 db). Vector symbols represent the large-scale, long-term, mean geostrophic currents. Speed is scaled according to the key on the chart.

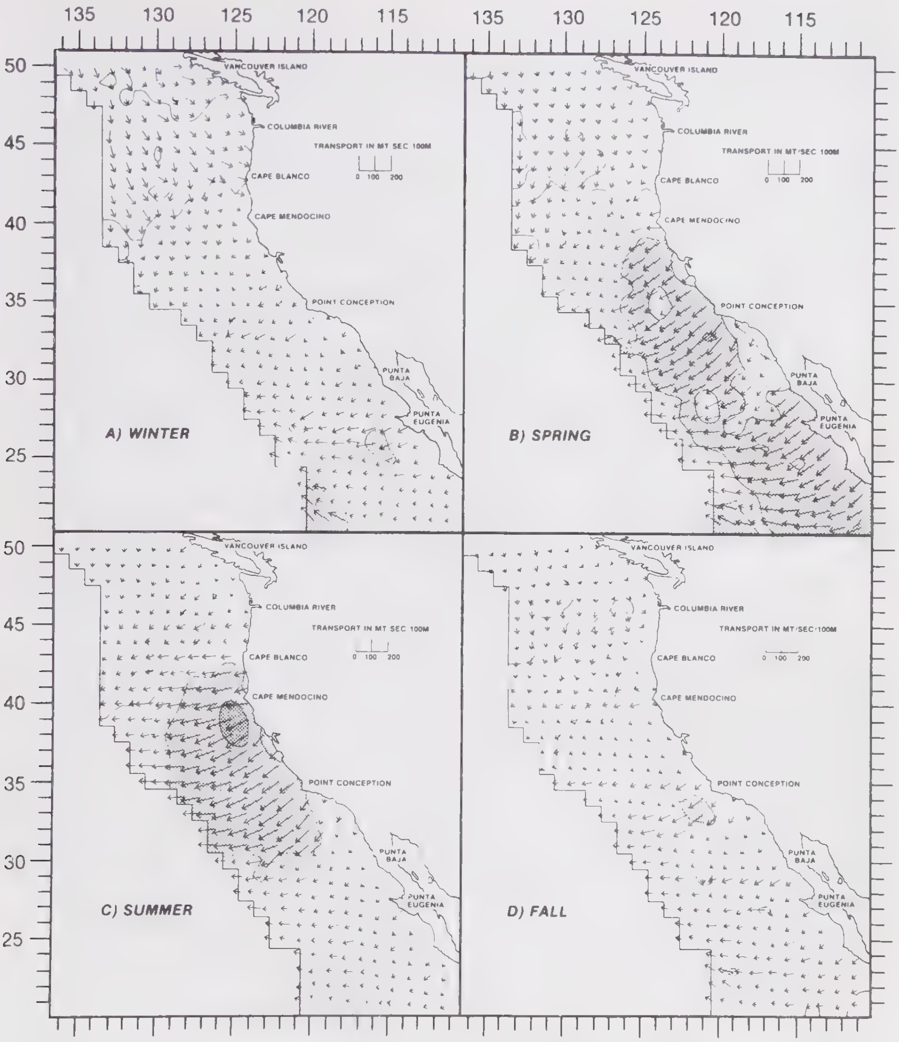

FIGURE 2. Surface Ekman transport: A. winter (December through February), B. spring (March through May), C. summer (June through August), D. fall (September through November). The contour interval is 50 t s^{-1} per 100 m width. Areas of transport greater than 100 t s^{-1} per 100 m are shaded.

Northern Hemisphere). The fine-scale vertical structure of the Ekman velocity field depends on vertical eddy viscosity characteristics, which are not well known; however, the total transport of water in the layer between the sea surface and the depth at which the drift velocities become negligible does not depend on these characteristics and can be inferred from the wind stress alone. The depth of negligible Ekman drift velocities is likewise not well known. However, most of the transport probably occurs in the upper 20 to 30 m; no appreciable Ekman drift is likely to penetrate beneath the surface mixed layer into the stratified portion of the water column. Therefore, the movement due to wind drift of aggregates of organisms that are mixed over a depth range as deep as or deeper than the Ekman layer generally corresponds to Ekman transport. The upper portion of the Ekman layer would tend to move in a direction closer to that of the wind stress, and so organisms that can maintain themselves at depths very near the surface might be moved at angles less than the full 90° to the right of the wind (i.e., somewhat to the left of the vectors in Figure 2). However, Ekman theory would have even the very surface of the ocean moving no less than 45° to the right of the wind, and so reference to the Ekman transport vectors will generally provide a sufficiently precise indication of onshore or offshore surface transport.

During winter (Figure 2A), Ekman transport is directed toward the coast in the Pacific Northwest region. South of Cape Mendocino the transport is offshore and increases in strength to a maximum south of Punta Baja, Baja California. By spring (Figure 2B), onshore Ekman transport in the north has relaxed and offshore transport has strengthened along the coasts of California and Baja California. Within the Southern California Bight, there is a local minimum in offshore transport. In summer (Figure 2C), the region of maximum offshore transport shifts north to northern California, and offshore transport occurs throughout the region. Transport off central Baja California has diminished considerably from the spring situation.During fall (Figure 2D), offshore transport relaxes off California. The mean surface drift becomes onshore north of Cape Blanco. The Southern California Bight continues to be an area of reduced offshore wind drift, as it is throughout the year. A discussion of the atmospheric features responsible for these seasonal wind drift patterns can be found in Nelson (1977).

The geostrophic flow data (Figure 1) yield velocities of water motion. However, the Ekman drift computations (Figure 2) yield mass transports averaged over the effective vertical thickness of the Ekman layer. Proper vector addition of the two flow components requires knowledge of the Ekman layer thickness, which is lacking. Equal vector symbol lengths in Figures 1 and 2 would indicate equal velocity contributions, assuming an effective Ekman depth of 25 m, a reasonable (Neumann and Pierson, 1966) but arbitrary choice. For example, Peterson et al. (1979) deduced a thinner Ekman layer of 5 to 15 m from their observations of copepod distributions off Oregon. For a thinner Ekman layer, the velocities corresponding to a given transport value would be proportionately larger, and for a thicker layer proportionately less. The long-term composite geostrophic flow fields (Figure 1) are, of course, highly smoothed representations. Any synoptic distribution would contain much more spatial detail, with local speeds ranging an order of magnitude greater (Wyllie, 1966).

Shorter Scale Flow Variations

Within the California Current, spawning tends to be distributed in both time and space. In addition, eggs and larvae may drift in the plankton for a considerable period after being spawned. Thus, small-scale flow fluctuations tend to be integrated by the time–space continuum of drifting larvae. The flow variations likely to cause year-class fluctuations by affecting overall reproductive success are those of large enough scale so that their effects are not averaged out. Such large time and space scale variations conform well to the simple Ekman–geostrophic model described in the previous section.

Instantaneous flow in the ocean is turbulent and approaches the Ekman–geostrophic model only in a large-scale mean sense. Any particular flow measurement could well be in complete nonconformity with the model. An appreciation of the scales of actual motion in the California Current can be gained from infrared photographs taken from earth-orbiting satellites, particularly during the upwelling season (Figure 3). Cold upwelled water (light gray shades) adjacent to the coast appears to be swept far offshore in large eddies and plumelike structures of up to several hundred kilometers in width. Sharp contrast with adjacent warmer surface waters (darker gray shades) is maintained over large distances, indicating transport of surface water at much higher speeds than the large-scale averages (Figures 1, 2). The large eddies are relatively deep features embedded in the geostrophic current field (Bernstein et al., 1977).

Even higher frequency variability characterizes the surface wind drift. Spectra of nearshore surface winds show a pronounced diurnal

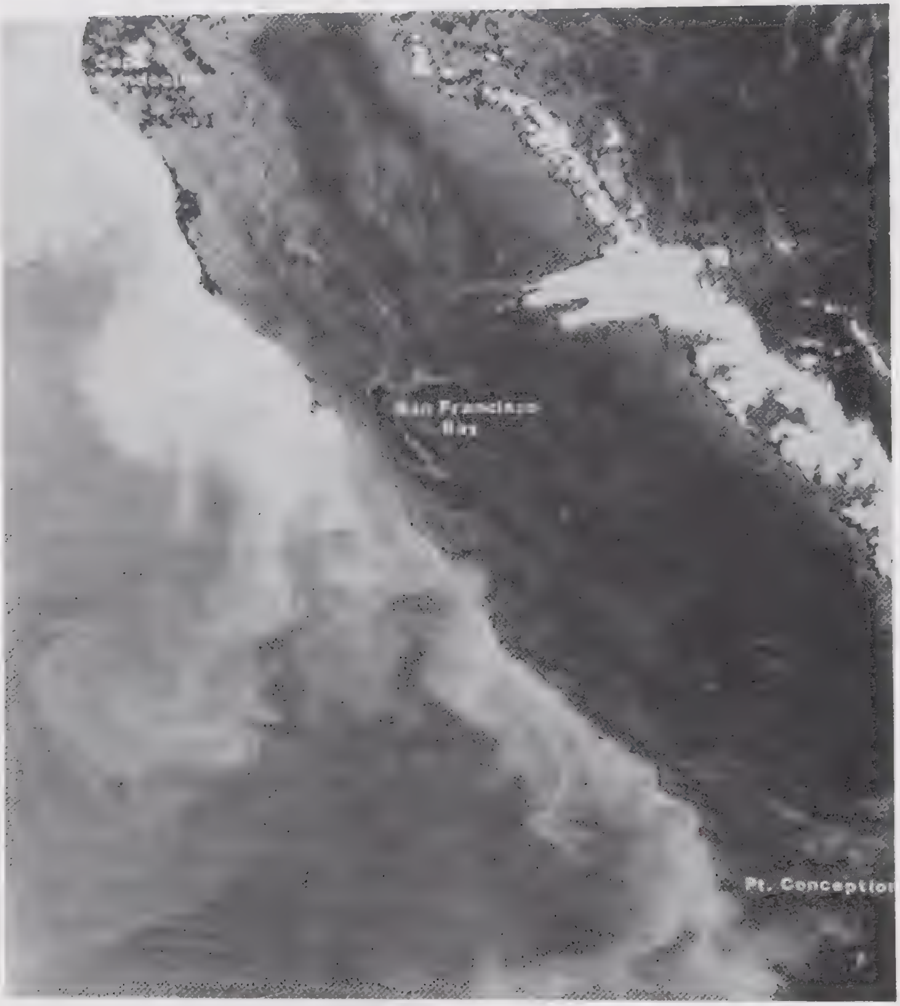

FIGURE 3. Infrared photograph of the California coast and the adjacent ocean taken from the NOAA-5 satellite on May 30, 1978. Cooler temperatures are indicated by lighter gray shades, warmer temperatures by darker shades. The filamentous patterns near the coast reflect the sea-surface temperature structure. Other whitish areas in the picture reflect snow on mountain tops and the cold upper surfaces of clouds. Photo supplied by NOAA/NESS Satellite Field Services Station, Redwood City, California.

periodicity and a large amount of variance on the "event" time scale, ranging from two days to several weeks (Bakun and Nelson, 1977). Off the Pacific Northwest, winter is marked by strong onshore-directed wind-driven transport events interspersed with relatively weak offshore transport episodes (Figure 4); relatively weak offshore transport characterizes summer. South of Cape Mendocino, the trend is for progressively less predominance of onshore transport during winter and stronger offshore transport during summer. The most energetic pulses of offshore transport occur off northern California during spring and summer. Off Baja California, a more continuous but less intense level of offshore surface wind drift is maintained throughout the year; here, the maximum tends to be in spring rather than in summer, as is the case farther north.

To the extent that these shorter scales of motion are self-cancelling and do not contribute to the larger scales, their net effect on the distribution of drifting larvae is to spread and mix the distributions in a manner somewhat analogous to turbulent diffusion. In this way, certain individuals could be transported counter to the longer-term displacement of the total larval biomass. Small-scale details of the flow on the continental shelf are lacking in our presentation. It is possible that unresolved features in the shelf circulation would not be self-cancelling on longer time scales. Considerable work near the Oregon coast (Smith, 1974) has indicated rapidly fluctuating alongshore geostrophic flow responding to variations in the local wind. However, the onshore–offshore component of flow is apparently much less energetic and resembles the large-scale Ekman transport.

Convergence, Divergence, and Upwelling

Where the surface wind drift is directed offshore the result is divergence next to the coast, since there is no possibility of a balancing wind drift from the solid continent. To the extent that coastal divergence cannot be compensated by convergence in the other components of horizontal flow, the result is a net loss of surface waters next to the coast. Conservation of mass requires the upward pumping of deeper waters, known as coastal upwelling. The converse process, where coastal convergence due to onshore surface drift leads to a downward intrusion of surface waters, is often referred to as downwelling.

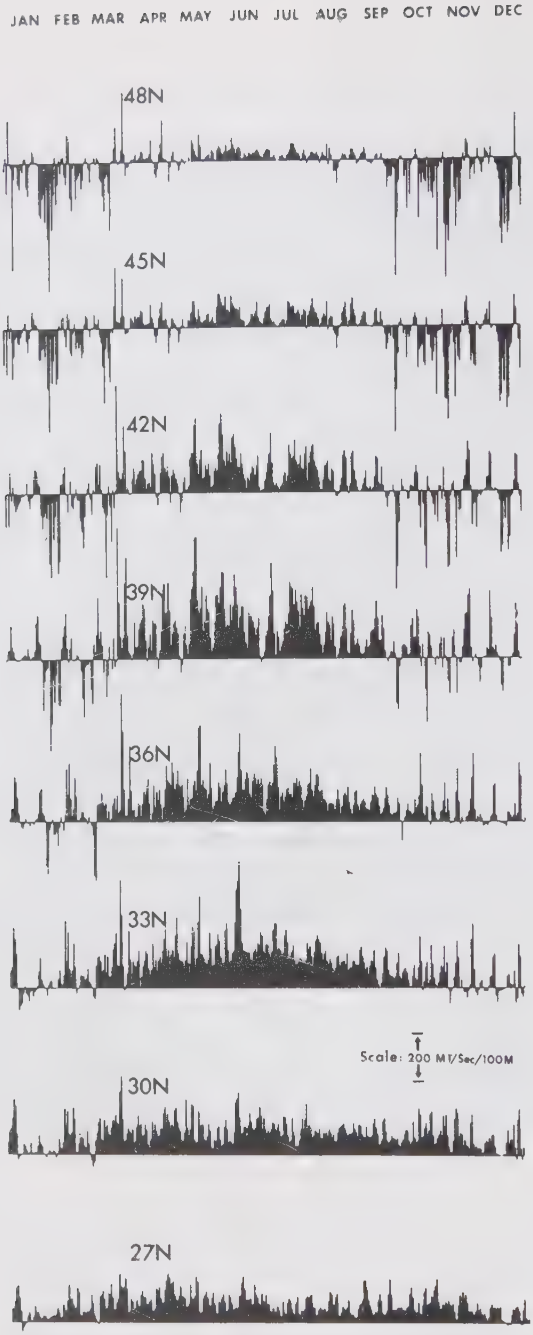

FIGURE 4. Daily upwelling indices for 1975 at 3° intervals from the coast of Washington to central Baja California. The magnitude of the offshore Ekman transport is indicated by the length of the bars. The scale is shown on the figure. Units are t s^{-1} per 100 m length of coast. Bars extending upward indicate offshore Ekman transport (coastal upwelling). Those extending downward indicate onshore Ekman transport (coastal downwelling).

The seasonal coastal upwelling cycle is well described by the drift patterns shown in the Ekman transport distributions (Figure 2). Conditions favorable to coastal upwelling continue throughout the year off Baja California; maximum intensity occurs during spring. Off the Pacific Northwest the upwelling season is largely confined to summer; winter is characterized by vigorous downwelling. The apparent effects of coastal upwelling are less obvious in the Southern California Bight than in the regions to the north or to the south (Bakun et al., 1974; Bakun and Nelson, 1977). The offshore extent of the primary coastal upwelling region is on the order of 10 to 20 km (Mooers and Allen, 1973), although under certain circumstances continental shelf topography may cause seaward expansion of this offshore scale (Huyer, 1976). Although the solid coastal boundary obviously affords the condition for the most intense divergence or convergence of surface drift, some convergence and divergence will occur whenever horizontal variation in the wind results in transport gradients along the direction of flow. Offshore areas of surface convergence would tend to concentrate near-surface planktonic material; accumulation of material in fronts and coalescence of patches would be favored. Areas of surface divergence would favor dispersion of planktonic organisms and diffusion of patch structure.

The tendency for convergence or divergence in the surface Ekman layer is controlled by the wind stress curl (Fofonoff, 1963). In the Northern Hemisphere, positive wind stress curl induces Ekman layer divergence; negative wind stress curl induces Ekman layer convergence. Quarterly distributions of wind stress curl (Figure 5) were constructed from Nelson's (1977) monthly distributions. Some of the small-scale detail in these patterns can be attributed to sampling error. However, major features are consistent and certainly significant.

Negative wind stress curl (surface convergence) predominates in the offshore region throughout the year. From this offshore region, a lobe of negative wind stress curl extends shoreward and impinges on the central Baja California coast between Punta Baja and Punta Eugenia. This feature appears consistently during all seasons. In this same area there is a consistent local maximum in the offshore Ekman transport (Bakun and Nelson, 1977). Directly adjacent to the coast the strong coastal boundary effect overrides the weaker surface Ekman convergence related to negative wind stress curl. Thus, coastal divergence and upwelling characterize the coastal boundary zone. However, offshore of the boundary zone surface convergence predominates. The situation from

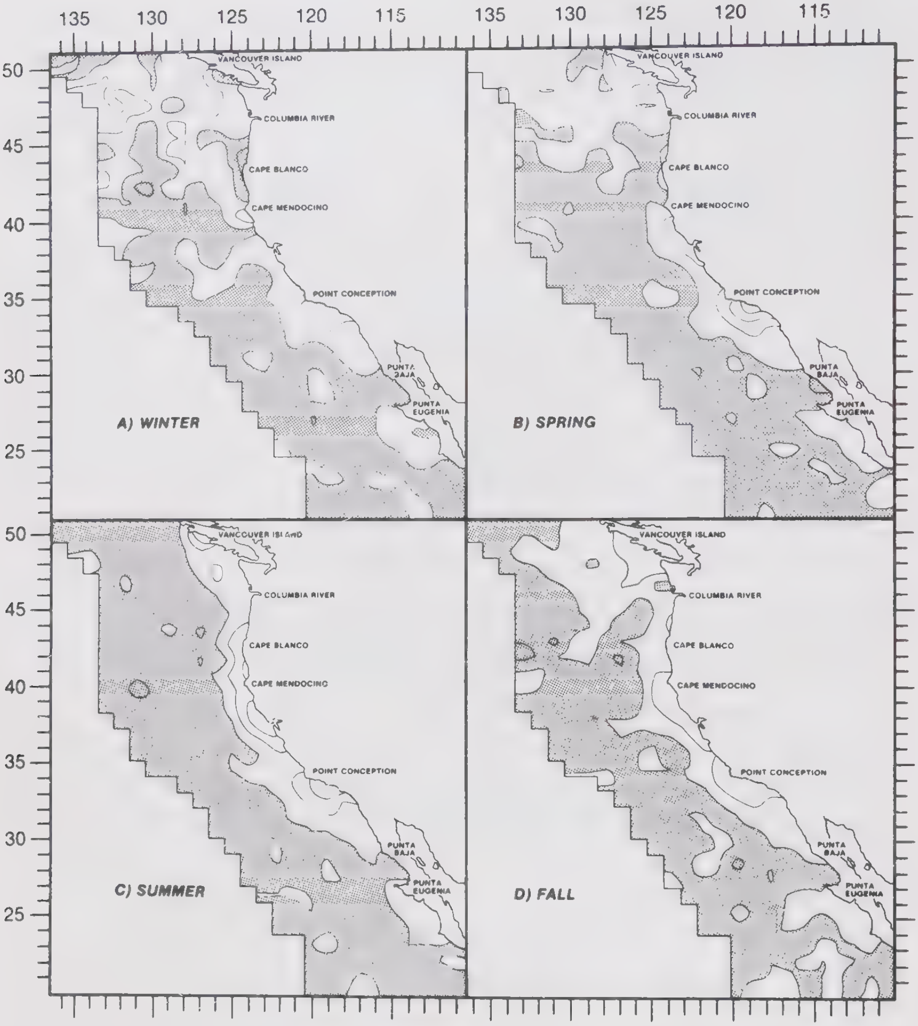

FIGURE 5. Wind stress curl: A. winter (December through February), B. spring (March through May), C. summer (June through August), D. fall (September through November). The contour interval is 0.25 dyne cm^{-2} per 100 km. Negative values are shaded and indicate surface Ekman convergence. Unshaded areas indicate surface Ekman divergence.

Punta Baja to Punta Eugenia is thus one of vigorous upwelling very near the coast, with convergence and downwelling beginning 10 to 20 km from the coast and extending to the offshore region.

To the north and south of this lobe of negative curl, regions of positive wind stress curl (surface divergence) extend from the coast to 100 to 300 km offshore. These are also consistent features, appearing in all of Nelson's (1977) monthly distributions. Ekman transport is generally directed offshore in both areas (Figure 2); the coastal boundary zone is characterized by divergence and coastal upwelling. Seaward of the boundary zone a continued level of divergence and upwelling extends offshore to the region where negative curl (convergence) predominates. Particularly strong positive curl characterizes the Southern California Bight. This strong positive curl area expands northward, following the seasonal northward progression of coastal upwelling, to occupy virtually the entire coast during summer. Vigorous coastal upwelling nearshore, accompanied by continued lower intensity upwelling offshore of the narrow coastal boundary zone, appears to be the most typical situation in the California Current.

Larval Transport and Reproductive Success

The preceding descriptions of the mean geostrophic flow, Ekman transport, and wind stress curl patterns in the California Current System suggest that, for purposes of larval transport, the system can be divided into four regions:

(1) The Pacific Northwest region (i.e., from Vancouver Island to Cape Blanco),
(2) The region of maximum upwelling (i.e., from Cape Blanco to Point Conception),
(3) The Southern California Bight (i.e., from Point Conception to Punta Eugenia),
(4) The southern Baja California region.

These four oceanographic regions are almost identical to the faunal regions described by Dana (1852) on the basis of temperature. The boundaries between the southern three regions correspond well with those used by most of the later biogeographers (Hedgpeth, 1957; Peden and Wilson, 1976; Horn and Allen, 1978). However, the separation of the Pacific Northwest and maximum upwelling regions into distinct faunal regions is not supported by recent zoogeographic studies based on extreme ranges. Horn and Allen (1978), who considered only the California fauna, did not find a faunal break at Cape Blanco, whereas Peden and Wilson (1976), who did not limit their study to fishes recorded in California, found a minor faunal break at Cape Blanco. The fact that the boundaries of these oceanographic regions may or may not agree with faunal breaks established by zoogeographic studies based on extreme ranges of species is not pertinent to this study. We are concerned with the relationships between reproductive strategies and oceanographic conditions on the spawning grounds of the dominant exploitable fishes in the California Current System. Furthermore, distributions of significant reproductive populations are imprecisely measured by zoogeographical regions based on range limits (Steinbeck and Ricketts, 1941:293–297; Peden and Wilson, 1976).

The Region of Maximum Upwelling

The surface circulation in the region between Cape Blanco and Point Conception is a logical explanation for the biological paradox that occurs here; the region is characterized by extensive upwelling, but also by low catches of resident fishes (Table 1). The fisheries and exploitable biomass of this region have been dominated by migratory pelagic stocks (sardine, *Sardinops sagax,* hake, *Merluccius productus,* and jack mackerel, *Trachurus symmetricus),* which spawn in the Southern California Bight. Young sardine, hake, and, to a lesser extent, jack mackerel are most abundant in central California, well south of the upwelling maximum at Cape Mendocino. Older sardine, hake, and jack mackerel are seasonally most abundant in the Pacific Northwest (Murphy, 1966; Alverson and Larkins, 1969; Blunt, 1969). The largest resident group of exploitable fishes in the region of maximum upwelling (*Sebastes*) has a local minimum in abundance near Cape Mendocino; peak abundance occurs in central California and in the Pacific Northwest (Gunderson and Sample, 1980). The largest resident stock in this region, shortbelly rockfish, *Sebastes jordani,* is found in central California. This is a pelagic species that has some life history features similar to clupeids (Lenarz, 1980). Stocks that feed in the region of surface convergence offshore (albacore, *Thunnus alalunga,* saury, *Cololabis saira,* and squids) are also relatively large compared to the resident coastal stocks.

Although the biomass of exploitable fishes is dominated by migratory stocks, the majority of the fish fauna are resident species that have various reproductive strategies that could reduce the advective loss of reproductive products. For example, demersal spawning in protected inshore waters occurs in herring, *Clupea harengus,* lingcod, *Ophiodon elongatus,* cottids, hexagrammids, stichaeids, and most of the other intertidal and littoral fishes of this region. Other strategies include live-bearing (rockfishes and embiotocids), anadromous spawning (salmonids and some osmerids), and deep-water spawning (some pleuronectids and sablefish, *Anoplopoma fimbria*). Another prevalent strategy, which reduces the advective loss of eggs and larvae, is spawning during winter and spring when onshore Ekman transport is most likely to occur in this region. The life history descriptions in Hart (1973) show that the majority of the fishes in the region of maximum upwelling and in the Pacific Northwest have a late winter–early spring spawning season, with peak spawning usually in February and March.[3]

There are fewer published data on larval fish in the region of maximum upwelling than in either the Pacific Northwest or Southern California Bight regions. However, at least in the southern portion of the region of maximum upwelling there appears to be a single peak in the inshore larval fish abundance. Icanberry et al. (1978) showed that maximum larval density occurred in February, and larval densities were high from January to March. This period of larval abundance was associated with low ocean temperatures and the onset of coastal upwelling. The density of larvae inshore declined sharply in March and April as the upwelling season developed.

There are three features in this region that could aid in the inshore retention of pelagic eggs and larvae. The first is the winter occurrence of onshore Ekman transport events, which are related to those that occur in the Pacific Northwest region. These events occur in the northern portion of the region of maximum upwelling, although they are usually of lesser magnitude than in the Pacific Northwest region. In central California the onshore events are less common and of shorter duration (Figure 4; lat. 36° N). The second feature is the shallow nature of the nearshore geostrophic flow in this region. Advection of organisms by both Ekman and geostrophic components of flow is dependent on their depth in the water column. Planktonic eggs and larvae in the upper mixed layer are highly susceptible to dispersion. Deep-water spawning and vertical migration of larvae are likely mechanisms for reducing the advective loss of eggs and larvae. Seliverstov (1974) has shown that larvae of the Atlanto-Scandian herring have diurnal vertical migrations as large as 75 to 100 m, and that regular diurnal migrations begin after the larvae have started feeding, six to nine days after hatching (8.8–10.8 mm). The third feature is the occurrence of eddies (Figure 3), which could return larvae to the inshore region.

The Pacific Northwest Region

In comparison with the region of maximum upwelling, offshore Ekman transport is weaker and of shorter duration in the Pacific Northwest region. Advective loss of reproductive products from the inshore region would therefore not be expected to be as severe as in the region of maximum upwelling. The faunas of the two regions are similar, with the exception that the Pacific Northwest has stocks of anchovy, *Engraulis mordax,* and hake, which reproduce within the region. The northern stock of anchovy spawns during the peak of the upwelling season (June and July), and its spawning area lies about 50 to 80 km offshore between lat. 44°N and 47°N. This spawning ground lies in an area of relative stability associated with the Columbia River plume (Richardson, 1973). This is also a region of relatively weak mean geostrophic flow (Figure 1) that lies to the north of the region of maximum upwelling (Figure 2C).

In their analysis of coastal and oceanic fish larvae over the Oregon continental shelf, Richardson and Pearcy (1977) delineated inshore and offshore larval assemblages. The inshore assemblage was dominated by spring spawners, particularly the osmerids, which spawn demersal eggs in very shallow water, and pleuronectids. Osmerid larvae primarily occurred near the bottom (100 to 150 m) by day and night, a feature that would reduce advective loss by surface transport. Offshore Ekman transport is minimal directly adjacent to a coastal boundary, and thus fishes that spawn in extreme inshore areas may be less subject to offshore transport. The offshore assemblage was dominated by livebearing rockfishes *(Sebastes)* and by midwater fish larvae. The rockfish spawn primarily in the late winter and early spring when onshore transport prevails. Midwater fish larvae are not expected to conform to the hypotheses presented here.

Pearcy et al. (1977) have shown that at least two northwest flatfish, Dover sole, *Microstomus pacificus,* and rex sole, *Glyptocephalus zachirus,* have larvae that are planktonic for a full year. Both of these fish are late winter–early spring spawners. Smaller larvae are found both inshore and offshore, but larger larvae are most common in waters beyond the continental shelf. During winter there is an increase in the proportion of the largest larvae over the shelf and slope where they will settle. When viewed from the perspective of the present work, the results of Pearcy et al. (1977) suggest that Dover and rex sole larvae are transported offshore during the upwelling season and are then returned onshore during winter when transient winter storms result in strong pulses of onshore transport. This hypothesis is strengthened by the work of Hayman (1978), who compared a wide range of environmental factors with year-class size in Dover sole and found that recruitment was best described by two wind-related indices. Increased recruitment was associated with reduced offshore Ekman transport during the upwelling maximum in June and July and with weak divergence, or convergence, during the December and January settling period.

The Southern California Bight

The Southern California Bight is characterized by minimal offshore Ekman transport (Figure 2) overlying a geostrophic flow pattern that features a closed gyral circulation near the coast (Reid et al., 1958) and an onshore component of flow farther offshore (Figure 1); seaward dispersion of reproductive products would appear to be minimized. The dominant pelagic fishes of the California Current (i.e., those that have supported large fisheries) all spawn in this region. The sardine, hake, jack mackerel, and, to a lesser extent, the Pacific mackerel, *Scomber japonicus,* and bonito, *Sarda chiliensis,* migrate into the region of maximum upwelling off central and northern California and into the Pacific Northwest for feeding. Because of limited swimming ability associated with small size, the central stock of northern anchovy is principally resident within the Southern California Bight, although tagging studies show that a small portion of the stock migrates as far north as central California (Messersmith, 1969).

The Southern California Bight differs from the regions to the north in that standing stocks of zooplankton are much smaller (Smith, 1978). Given favorable transport conditions, food limitation during critical larval stages may regulate reproductive success. Anchovy and hake have peak spawning in late winter (January to March). In this region the winds are normally much weaker in the winter than in the spring or summer. Lasker (1975, 1978) has suggested that successful feeding of early anchovy larvae is dependent on chlorophyll maximum layers, which only exist in the absence of storm-driven turbulence. Sardine, Pacific mackerel, jack mackerel, bonito, and barracuda, *Sphyraena argentea*, have peak spawning seasons during the period of maximum upwelling (May and June). Arthur (1976) has shown that the diet of anchovy larvae is dominated by phytoplankton (dinoflagellates) and early copepod stages, but that larval sardines and larval jack mackerel feed almost exclusively on the early stages of copepods. The other species that spawn during the upwelling maximum probably also have larval feeding preferences for copepods. The development of concentrations of forage for the early fish larvae would therefore be largely dependent upon upwelling-related meteorological conditions prior to and during the spawning periods. Upwelling prior to the spawning period would increase primary productivity and result in copepod reproduction. Upwelling during the spawning peak would disperse both fish larvae and forage.

Parrish and MacCall (1978) have related recruitment in the Pacific mackerel stock to upwelling. Their model, which includes offshore Ekman transport, wind stress curl, and a Ricker density function, accounts for 76% of the variation in recruitment from 1946 to 1968. Upwelling one month prior to spawning was much better correlated with recruitment than was upwelling during the spawning period. The one-month lag may represent the time scale for the development of a copepod bloom following increased nutrient enrichment.

Arthur's (1977) description of the microcopepods of the California Current System shows that the zone of maximum nauplii concentration is seaward of the Channel Islands, about 100 to 300 km off the coast. He states that the average nauplii maximum approaches the coast south of

San Diego and is adjacent to the coast in northern Baja California. We suggest that this zone of maximum nauplii is associated with maximum geostrophic flow (i.e., nutrient-and plankton-rich water from the north) and the inner edge of the negative wind stress curl region (i.e., concentration of plankton by surface convergence).

The Southern Baja California Region

The lobe of negative wind stress curl that impinges on the coast between Punta Baja and Punta Eugenia (Figure 5) separates distinct oceanographic regimes. Off southern Baja California a cyclonic gyre appears during fall, when upwelling is most relaxed. During spring the upwelling-induced southward flow tends to obscure this circulation (Bakun and Nelson, 1977). Due to this seasonality, the feature is not strongly evident in the annual mean geostrophic flow pattern (Figure 1). The southern Baja California region is also separated from the Southern California Bight region by the central Baja California upwelling maximum, which is centered near Punta Baja and extends south of Punta Eugenia. A number of pelagic fishes have subpopulations off southern Baja California that are distinct from those in the Southern California Bight region. These include sardine (Clark, 1947), Pacific mackerel (Roedel, 1952), and northern anchovy (Vrooman and Smith, 1971)

Warm water advection near the coast associated with cyclonic circulation and the proximity to the warm Gulf of California results in a large tropical component in the fauna. The most obvious pelagic form is the galatheid, *Pleuroncodes planipes,* which is extremely numerous in this region (Longhurst, 1967). Tropical clupeids, engraulids, and carangids are also common (i.e., thread herring, *Opisthonema medirastre,* anchoveta, *Cetengraulis mysticetus,* and Mexican scad, *Decapterus hypodus*). Much of this tropical fauna does not extend to the region of strong upwelling near Punta Baja, and the faunal ''front'' between the tropical and subtropical faunas occurs in the vicinity of Magdalena Bay (Ahlstrom, pers. comm.[4])

Discussion

A general pattern of correspondence between reproductive strategies and ocean flow characteristics has emerged. The indication is that the necessity for minimization of offshore loss of reproductive products by seaward transport processes must have exerted a particularly strong control on the development of seasonal and geographical spawning characteristics. This, in turn, implies an important effect of transport conditions upon reproductive success, leading directly to the hypothesis that deviations from ''normal'' transport conditions, to which reproductive strategies are adapted, may be a cause of the very large recruitment variations observed in the important coastal fisheries of the California Current.

Large deviations from mean seasonal surface transport conditions are known to occur. Charts of geostrophic currents computed from oceanographic surveys (e.g., Wyllie, 1966) show definite inter-year differences, although methods for quantifying the effects on biological scales are not yet well developed. However, in situations where the geostrophic flow tends to parallel the coast, it is less important in terms of this particular hypothesis than the surface Ekman transport. Offshore transport is more likely to be unfavorable to larval survival than alongshore transport, because the habitat changes more rapidly in the offshore direction than in the alongshore plane. In addition, surface Ekman transport has greatest variability in the onshore–offshore component. Bakun's (1973, 1975) upwelling indices are one attempt at quantifying this effect. At any given location, general seasonal characteristics are maintained from year to year; however, large inter-year differences in seasonal onset, intensity, duration, and properties of short-scale fluctuations are apparent.

Upwelling is also a major mechanism for surface nutrient replacement, which makes the California Current a productive region. Upwelling, therefore, can have favorable and unfavorable aspects. If upwelling events occur prior to a species spawning period it is likely to aid larval survival. If it occurs during the peak of spawning its effects are more likely to be detrimental.

The effects of upwelling on larval survival may also differ geographically. In the region of maximum upwelling between Cape Blanco and Point Conception, larval survival seems more likely to be transport limited than food limited. Conversely, in the upwelling minimum within the Southern California Bight, larval survival may be more likely to be food limited.

Analysis of varved sediments in the Southern California Bight (Soutar and Isaacs, 1974) has shown that the biomass of the major pelagic spawning stocks and, indeed, the total biomass of the combined stocks are subject to large, long-term fluctuations. The two species most likely to be in competition as adults (anchovy and sardine) show no relationship between their stock sizes over a 200-year period. The two species most likely to be in competition as larvae, the sardine and the Pacific mackerel, show considerable similarity in their population fluctuations (Smith, 1978).

Short-term environmental variations or longer-term climatic trends could favor winter spawners (hake and anchovy), spring spawners (sardine and the mackerels), both, or neither. Anchovy might capitalize on good conditions whenever they occur due to its low level, year-round spawning. Individual years with reduced upwelling, such as 1967 (Bakun, 1975), undoubtedly lower the productivity of the system and would therefore affect the adults of all the pelagic species. However, the reduced vertical circulation would result in stability of the water column, which has been associated with good reproductive success of anchovy (Lasker, 1978). Reduced vertical circulation might therefore be expected to produce moderate stocks of anchovy (and perhaps hake, which has peak spawning at essentially the same time as anchovy). A scenario might be: series of years with reduced upwelling in the Southern California Bight region, such as 1964–1968 (Bakun, 1973), would be expected to result in a sharp decrease in the total standing stock of the spring spawners due to poor recruitment. Adult growth of winter spawners would be poor, but recruitment might be favorable due to stability during their spawning season. The anchovy and hake stocks would therefore be expected to be at moderate levels following a run of years such as that occurring in 1964–1968. This is consistent with analyses of scales deposited in sediments, which show that populations of anchovy and hake are much less variable than those of sardine and Pacific mackerel (Smith, 1978).

If population size is largely determined by a highly variable larval survival rate, the conclusion is that the adult population seldom reaches a food-limited carrying capacity. If the stocks were originally near adult carrying capacity, there should be a compensatory alteration in growth and reproductive rates when the stocks are reduced by fishing. Four extensively studied stocks (sardine, Pacific mackerel, anchovy, and Pacific ocean perch, *Sebastes alutus*) have had extensive fluctuations in population size. Knaggs and Parrish (1973) have shown that there were no significant changes in the growth of Pacific mackerel associated with stock size. In the sardine stock the 0-age group, which was largely confined to the relatively plankton poor Southern California Bight, showed increased growth associated with smaller stock size (Iles, 1973). The older fish that made feeding migrations into the region of maximum upwelling and the Pacific Northwest region showed no significant changes in length associated with stock size; changes in the condition factor (relative fatness) have been associated with stock size (MacGregor, 1959). No changes in growth rates have been found in the numerous studies that have been published on the northern anchovy and Pacific ocean perch. There are some indications of density-dependent changes in reproduction. The proportion of sardines that spawn at age two and the proportion of Pacific mackerel that spawn at age one increased as the stocks declined (Murphy, 1966; Parrish and MacCall, 1978). However, stock-recruitment relationships for sardine (MacCall, 1979) and Pacific mackerel (Parrish and MacCall, 1978) show large variations with very little density dependence. Gunderson (1977) has suggested that Pacific ocean perch have a relatively flat spawner-recruit curve. MacCall's (1980) logistic growth-rate curve for the central anchovy stock is quite flat, and MacCall suggests that abundance in any given year is determined more by natural variations in recruitment than by the fishery. The minor nature of the observed density-dependent changes in growth and reproductive rates strengthens the suggestion that carrying capacity for adults is seldom a limiting factor in the major fish stocks of the California Current.

A major problem in defining the environmental-biological relations that are required to construct useful predictive models for fishery management is that there are generally only short time series with which to work. Fishery data characteristically yield one data point per year, and the period over which the time series can be considered homogeneous does not normally exceed 10 to 20 years. To sort out a multitude of possible environmental effects from a series with 10 to 20 data points is obviously a statistically impossible task. Therefore, it is necessary either to find the means to reduce the environmental factors to one, or at most several, indices of integrated environmental state, or to hope that one, or perhaps two, environmental factors will have such a dominant effect as to be discernible through the "noise level" generated by the other environmental effects. The considerations presented in this paper suggest that surface drift during the early egg and larval period may be such a dominant environmental factor for some of the major coastal fishery species of the California Current.

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The original motivation for this comparison of transport patterns and reproductive strategies was provided by E. H. Ahlstrom's comment that in the California Current region fishes with northern affinities tend to be winter spawners and fishes with southern affinities tend to be spring spawners.

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Notes

1. Personal communication, G. C. Broadhead, Living Marine Resources, Inc., 7169 Construction Court, San Diego, California 92121.

2. Personal Communication, T. Dark, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, Seattle, Washington 98115.

3. This same suite of reproductive strategies occurs in tropical marine fishes associated with coral reef, mangrove, and tropical seagrass communities (Johannes, 1978).

4. Personal communication, E. H. Ahlstrom (deceased), Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, California 92037.

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Annex H

Report of the Sub-Committee on Small Cetaceans

1. PARTICIPANTS, AGENDA AND INTRODUCTORY REMARKS

The meeting was chaired and the report edited by Perrin. Members (M) of the Scientific Committee of the IWC, invited experts (E), and observers (O) attending were:

Allen, R. (E), Anderson (M), van Beek (M), Berney (O), Best (M), Braham (M), Brodie (M), Brownell (M), Carr (M), Chen (E), Gordon-Clarke (O), Ikeda (M), Ivashin (M), Jordan (O), Klinowska (M), Kapel (M), Kato (M), Mitchell (M), Ohsumi (M), Øritsland (M), Rudge (M), Sharov (M), Spong (O), Terekhin (M) and Yoshinari (M).

Some participants did not attend all sessions of the meeting.

The draft agenda was discussed and approved with minor emendations (Appendix 1).

Klinowska, Braham, Allen, Anderson, Brownell and Øritsland acted as rapporteurs and chaired sub-groups.

2. DOCUMENTATION

Documents available to the sub-committee and containing information on small cetaceans were SC/32 ProgReps Australia, Canada, Denmark (Greenland), Japan, Norway, Seychelles, South Africa, UK, USSR and US; SC/32/SM 1–18; SC/32/O 1–3, 5, 9–11, 14 and 16; and issues LXXXIII and LXXIV and the provisional issue LXXXV of International Whaling Statistics.

3. REVIEW OF MANAGEMENT ACTIONS AND RESEARCH ON NORTHERN BOTTLENOSE WHALE, STRIPED DOLPHIN, DALL'S PORPOISE AND HARBOUR PORPOISE

3.1 Beginning in 1976, the sub-committee, the Scientific Committee and the Commission have urged that member nations initiate research on the substantial directed fisheries involving these species (recommendations for research outlined in *Rep. int. Whal. Commn* 27: 481). In one case, that of the bottlenose whale, a management action was recommended and implemented.

3.2 New information

3.2.1 Northern bottlenose whale, North Atlantic

Twenty-six bottlenose whales were seen in the northwest Atlantic and 32 in the central east Atlantic during a sea mammal sighting programme carried out on Soviet research cruises (SC/32/O 2). No other new data are available.

This species was provisionally listed as a Protection Stock for the entire North Atlantic in 1978, pending the accumulation of sufficient information and a thorough analysis of its status. It is noted that the bottlenose research programme recommended in 1977 in order to obtain independent stock estimates from special sighting cruises and research catches has still not been carried out. The Norwegian fishery for bottlenose whales ceased in 1972, and no new data are available on stocks.

3.2.2 Striped dolphin, Northwest Pacific

Directed fisheries for this species continue in Japan. Statistics presented in SC/32/ProgRep Japan show that in 1979 2,193 were taken in drive-in fisheries and 19 incidentally in fishing gear.

Kasuya (1976) estimated total population size in 1974 at 186–202,000, less than 50% of estimated original population of more than 404,000. He estimated MSY at 4,140–6,530 and sustainable yield in 1974 at 4,120–6,140. The take in 1974 was approximately 13,000. Kasuya's estimates were based on assumptions and models that need further examination. No stock assessment has been carried out subsequent to his analyses, although Miyazaki (1977) has developed new estimates of life-history parameters that very probably would change the outcome of such a re-assessment.

Although extensive biological and population studies have been carried out, several specific research needs identified in 1976 still remain (*Rep. int. Whal. Commn* 27: 481). These include collection of detailed effort statistics; tagging and census studies to obtain information on school structure, migration and definition of stocks; and monitoring life history parameters.

While catch statistics (by species and port only) were available this year for the first time, results of other components of the research programme announced last year (Appendix 6 to Annex I, *Rep. int. Whal. Commn* 30: 128) were not yet available to the sub-committee. Ohsumi reported that it has not yet been possible to fully implement the research plan announced last year; efforts to do so continue. The sub-committee re-emphasizes the need for this research.

3.2.3 Dall's porpoise, North Pacific

Populations of this species are subject to both direct and incidental take in the North Pacific. A 3-year joint programme of research by the US and Japan is in its third year, and analyses of data and specimens collected from incidental takes by Japanese salmon gillnetters and research vessels will be completed in June, 1981 (SC/32/SM8).

Incidental take in the salmon fisheries (including by research vessels) was 829 in 1978 and the same in 1979 (SC/32/SM9); the 1980 season is underway. Preliminary estimates of abundance in the Bering Sea, west-central North Pacific and Gulf of Alaska (approximately 3 million square miles), using a strip-transect model, range from about 0.8 million to about 1.8 million Ohsumi reported that Japan also presented an estimate of over 5 million at a recent meeting of the International North Pacific Fisheries Commission (INPFC). If the lowest of these estimates is of the correct order of magnitude and if it be assumed that a single interbreeding population inhabits the area surveyed, it seems likely that the incidental take alone will not have a measurable effect on abundance. The sub-committee, however, recognizes that more than one population may well be involved and believes that considerable research effort should be focused on the questions of possible geographical variation in morphology and of patterns of distribution and migration.

Dall's porpoise are also taken in directed fisheries in Japan. A programme of collection of detailed catch information begun last year (Appendix 6 to Annex I, *Rep. int. Whal. Commn* 30: 128) has yielded statistics for several types of fisheries (SC/32/ProgRep Japan). A total of 6,878 were taken in 1979. Kasuya (1975) estimated that a sustainable yield of 6,000 would require a population of 125–400,000, assuming natural mortality rate (M) of 0.050–0.075 and calving interval of three years. The size and status of the stock(s) are unknown. Data adequate for stock assessments were not available to the sub-committee.

3.2.4 Harbour porpoise, North Atlantic

This species is taken in directed fisheries and incidentally in gillnets in small numbers (SC/32/O 5). As was the case at the last meeting of the sub-committee (Annex I, *Rep. int. Whal. Commn* 30: 112) no estimates of take in the aboriginal fisheries in the Bay of Fundy and Grand Manan Island regions (US and Canada) were available to the sub-committee. The directed take in Greenland in 1979 was estimated at 900, (SC/32/ProgRep Denmark) up from 750 in 1978 but about the same as in 1977 (*Rep. int. Whal. Commn* 29: 115). The sub-committee continues to be concerned about the possible effects of this take in a restricted area, from a coastal population of unknown size and status. Some members of the sub-committee felt that the long-sustained catch (over the last 40 years) indicates that the stock has not been adversely affected. All the members of the sub-committee agreed, however, that the data necessary for a stock assessment are not available.

4. OTHER DIRECTED FISHERIES ON SMALL CETACEANS

4.1 Killer whale

4.1.1 Antarctica

In the 1979/80 Antarctic season the Soviet Union took 916 killer whales, which was a substantial increase over previous catches. The Soviet Union's effort in Antarctica is primarily directed at minke whales, and from 1954 to 1979 the average annual Antarctic catch of killer whales was only 28. At the 1979 meeting, the Scientific Committee recommended that the USSR be urged by the Commission to take no more than 24 killer whales from Antarctica in 1979/80. The Commission did not follow the recommendation.

4.1.1.1 Identity and status of stock (s)

There is an increasing amount of evidence for a complicated stock structure of killer whales, perhaps even down to the level of some genetic isolation among pods (SC/32/SM9). Two stock structures of Antarctic killer whales were suggested in SC/32/SM12: firstly, a division into six stocks on the basis of winter migrations to the east and west coasts of South America, Africa, and Australia; and secondly, on the basis of length composition of mature females, existence of a small form found most commonly in the Amundsen sea. Also, data on length frequencies are suggestive of a real difference (4.1.1.1.5 below), and Ivashin reported that recent studies of colour patterns have shown population differences in the Southern Hemisphere.

There is insufficient evidence on which to base geographical stock boundaries which would be of long-term use for assessments. The migration model does not give any indication of suitable boundaries in the Antarctic, where most exploitation takes place; and although a boundary of 120°W to 60°W might be inferred from SC/32/SM2 for the proposed smaller form there was no kill in this area in 1979 (SC/32/SM 9), nor are any data for stock assessment available. Thus the sub-committee is obliged to treat the Antarctic killer whales provisionally as if they are a single stock but to take the probable existence of more than one stock into account when proposing management measures.

4.1.1.2 Abundance

For Antarctic waters there are sightings data for the 1979/80 season (SC/32/ProgRep USSR) giving a sighting rate of 13.9 killer whales/CDW. This is about one third of the sighting rate observed during the same expedition for minke whales. However, without other information it is difficult to make abundance estimates using this type of data.

During the 1978/79 and 1979/80 IDCR southern minke whale assessment cruises, killer whale sightings data suitable for line-transect analysis were collected and have been analysed (SC/32/SM10). This analysis gives a population estimate in baleen Areas III and IV of 27,500, with a standard error of 6,038. In Appendix I an alternative analysis of the data by Allen is given which gives an estimate of 61,200. This population estimate was made for the areas shown in Fig. 1 and does not include animals known to be north of the surveyed area or those that may be in the pack ice to the south. Furthermore the estimate may be biased downwards, because all whales on the track line of the vessel may not be seen. The sub-committee accepted this estimate, with a 95% confidence interval of 30,600–81,800.

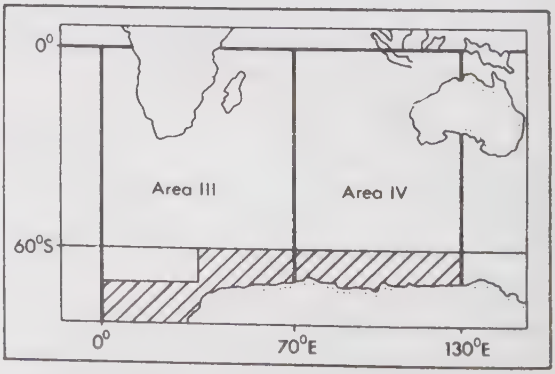

Fig. 1. Area included (shaded) in estimation of abundance of Antarctic killer whales.

4.1.1.3 Gross reproduction rates

SC/32/SM9 quotes estimates of reproductive rates of 'adult' (presumably sexually mature) females from the coastal waters of British Columbia of between 11.6–13.3%, and estimates of pregnancy rates of females taken by the Norwegian whaling fleet prior to 1976 of 13.3%. A gestation period of 12–16 months is reported from several authors, which implies a reproductive rate for adult females between 10 and 13%. Assuming that the proportion of reproductively active females in the population is 40% (SC/32/SM9) these data give gross reproductive rates for the population of between 4 and 5%.

Additional data in the form of proportions of females which are pregnant are now available from Antarctic whaling operations. These together with the assumptions of gestation period and the proportion of adult females are used to make additional estimates shown in the table below.

Source		Number of adult females	Number of pregnant females	Population gross reproductive rate
Antarctic	SC/32/SM12	91	25	8–11%
Antarctic 1979–80	SC/32/ProgRep USSR	333	141	13–17%

These rates are considerably higher than those reported in SC/32/SM9 and, if correct, would require very short reproductive cycles. In SC/32/SM10 there are data showing 51 calves (7–12 ft long) in a total of 785 animals which corresponds to a calf ratio of 6%. It is possible that some of these calves were older than one year, and that they had already been slightly reduced in number of mortality. Nevertheless, the sub-committee agreed that this rate was likely closer to the gross reproductive rate than the rates deduced from the samples of adult females which may not be representative of the population. The sub-committee concluded that the gross reproductive rate is likely to be in the range of 4–7%.

4.1.1.4 Natural mortality rate

Unfortunately the killer whales harvested in recent years have not been aged and there is no information from this source about natural mortality.

4.1.1.5 Catch composition

The length and sex compositions of the recent killer whale catches in Antarctic are given in Table 1.

These data show that sexes are represented evenly and with the exception of small (less than 14 ft) animals they appear to be spread over all sizes. There is a marked difference between males and females. The distributions can be compared with values quoted in SC/32/SM9: weaning at 14 ft, female sexual maturity at 16 ft, and male maturity at 22 ft. SC/32/SM12 gives a minimum length of maturity for females of 18 ft for animals thought to belong to a small form and states that size of female maturity of other killer whales was at a greater size. A figure of 21 ft was given for maturity of males in Antarctica.

Length frequencies for Antarctic catches by baleen Area are given in IWS (prov. LXXXV). These data also show clear differences among Areas III, IV and V and could either indicate stock differences or be sampling artifacts. Ivashin stated that he will endeavour to find out if the catches could have been selective.

4.1.1.6 Stock assessment

Because of the lack of estimates of natural mortality rates and the probable existence of several stocks that cannot at this time be defined, the sub-committee was unable to assess status of the stocks or deduce maximum net reproductive rates.

4.1.2 Norway

During 1979, Norway took 221 killer whales in Norwegian coastal waters. At its last meeting the Scientific Committee recommended that Norway limit its 1980 catch to 54 killer whales. The Commission did not follow the recommendation, but Norway did set a national catch limit of 54 for 1980. The number was taken in January this year, after which no more whaling for killer whales was permitted.

4.1.2.1 Stock identity

There is no information available about the stock structure of the killer whales in the North Atlantic.

4.1.2.2 Abundance

There were no data available to the sub-committee for making estimates of stock size(s).

4.1.2.3 Gross reproduction rates

In SC/32/SM14 there are data giving proportions of pregnant females in Norwegian catches. The table below is calculated using only females of 16 ft or larger and the same assumptions about gestation period and proportion of adult females in the stock as were used for the Antarctic killer whales.

Source	Number of adult females	Number of pregnant females	Population gross reproductive rate
Norway 1978 SC/32/SM14	29	18	19–25%
Norway 1979 SC/32/SM14	104	32	9–12%

The same reservations, mentioned for Antarctic killer whales above, were expressed about these apparently high reproductive rates by the sub-committee, which concluded that a range of 4–7% is more realistic.

4.1.2.4 Natural mortality

No estimate of natural mortality is available.

4.1.2.5 Catch composition

Table 1 shows length and sex composition for Norwegian catches in 1978 and 1979.

4.1.2.6 Stock assessment

No abundance estimate of the killer whales in Norwegian waters is available, and consequently stock assessment is not possible.

4.1.3 Research needs

At the 31st meeting the Scientific Committee recommended that the Commission request that Norway and USSR produce information necessary for an assessment of the killer whale stocks being exploited by their whalers.

In response to this request both countries supplied data on catches, including length and sex composition and information on whether or not females were pregnant. In addition the Soviet Union provided sightings data and detailed catch rates. Unfortunately these data can only be used for making estimates of population size when information for several years is available. The information that is still necessary before an adequate stock assessment can be made are estimates of abundance and natural mortality. The recent IDCR minke whale cruises have provided data for population estimates in part of Antarctica, and the sub-committee believes that this type of survey should be conducted for further stock assessment of exploited killer whales. The most direct means of obtaining natural mortality rates would be by ageing animals caught, and, as samples of teeth are taken, the sub-committee believes that reading these teeth is the first step in developing natural mortality estimates.

The stock structure, particularly in Antarctica, where there is some evidence for the existence of several stocks, is also an important issue. The sub-committee believes it is important that the issue of stocks should be addressed by the Soviet Union, and, until it is, all data should be reported by subareas of the Antarctic, such as areas bounded by 10° of longitude.

The Norwegian exploitation of killer whales is partly directed at reducing the predation of killer whales on herring stocks. To date there have been no papers presented to the Scientific Committee either documenting this predation or estimating its effect on the herring stocks. The sub-committee believes that Norwegian scientists should report on this at its next meeting.

It is possible that the Norwegian killer whales have been exploited at a relatively greater level than the Antarctic killer whales, and thus that comparison of reproductive rates may yield some information on the maximum net reproductive rates. The sub-committee believes it is very important to estimate reproductive rates from both areas.

The sub-committee recognises that valuable work on the social structure of killer whale groups is being carried out on the west coast of North America and in Argentina. The sub-committee supports this work and hopes that Canada and the United States will report on it at the next meeting.

The recent ICDR minke whale cruises have provided the first data which could be used to make a partial estimate of killer whale stock sizes in Antarctica. The sub-committee welcomes this type of research and believes that further cruises which collect line-transect data should be encouraged both in the unsurveyed areas of Antarctica and of the northeastern Atlantic.

4.2 White whale and narwhal

Investigation of the life history and status of these species is an important management problem, principally for several reasons described in last year's report.

4.2.1 White whale

4.2.1.1 Distribution, migration, definition of stocks and abundance

Following the conceptual model proposed by Perrin in 1979 (Fig. 2, *Rep. int. Whal. Commn* 30: 118) the sub-committee further evaluated the question of stock discreteness by reviewing the available information on geographical areas.

(1) *The Bering – Chukchi – Mackenzie stock(s) and the Cook Inlet stock.* A review of papers indicate that white whales in the Bering Sea move north along the west coast

Table 1

Length frequency of killer whales (SC/32/SM14, SC/32/SM12 and SC/32/ProgRep USSR)

	Norway 1978		Norway 1979		Antarctic 1961–78		Antarctic 1979/80	
ft	F	M	F	M	F	M	F	M
8		1		1				
9								
10	1	1		1			1	
11								
12	1		3	1			1	
13							3	1
14		2	3	1			6	1
15		1	8	1			9	4
16	5	2	15	5			25	6
17	7	1	28*	15	4	2	67	6
18	8*	5	18	18	10	7	45	14
19	5	4*	13	18*	11	10	60	39
20	2	5	14	11	20	21	82*	32
21		3	3	6	19*	17	86	52
22		4	2	10	26	14	55	69*
23	2	1		4	18	27	16	71
24				1	5	31*	2	45
25					3	33	1	39
26						24		23
27						13		9
28						5		14
29						1		21
30								1
	31	30	107	94	118	205	459	447

* Indicates median length.

of Alaska and east coast of the USSR from April through early summer (SC/32/SM13 and 18). On the USSR and US sides, summer resident white whales are common but not abundant along the coast. The winter distribution of this population is thought to be in the central and south-central Bering Sea loose pack ice and along the Soviet coast except for those animals remaining in Bristol Bay and resident in Cook Inlet, Alaska. The sub-committee urges that studies be directed at providing information on stock discreteness.

(2) *Far – North white whales of the Barents, Kara, White and Okhotsk Seas.* Two documents provided new information on Soviet white whale populations. From analysis of morphological data on white whales from the Far North, Ognetov (SC/32/SM1) concluded that animals inhabiting the White and Kara Seas are related, suggesting that they are one stock.

The number of white whales in the Sea of Okhotsk apparently suffered a large decline up to 1963, but no specific data or cause were described (SC/32/SM4). From a census conducted in July 1970, this population was estimated at 10,000–18,000 animals, although only 1,300 were actually seen. A survey in August 1979 of the same area resulted in only 160 sightings. Berzin (SC/32/SM4) speculated that the whales were further offshore, resulting in a lower count. Given the behaviour of summering white whales in other areas (i.e. generally coastal), the recent surveys suggest that the population may be further depleted. Population assessment studies are strongly urged.

(3) *The Davis Strait – Baffin Bay stock, Cumberland Sound stock, Gulf of St Lawrence stock and Hudson Bay stock(s).* There is no conclusive evidence to suggest that the Davis Strait and Baffin Bay white whale populations are separated into more than one stock, except perhaps for the West Hudson Bay group(s) (SC/32/O 16). Some mixing with adjacent groups for the Lancaster Sound, West Greenland, Hudson Bay/Strait and Cumberland Sound populations may occur in winter.

New information on white whales off Quebec (Southeast Hudson Bay) indicate that this population is composed of approximately 400 animals (SC/32/SM16). Apparently a major decline occurred historically, as a result of commercial hunting and increasing local human activities. The population in the Poste-de-la-Baleine area may be a local, year-round resident group with no apparent migration taking place except for local movements to selected areas for calving, rearing young and feeding (SC/32/SM16).

4.2.1.2 Age determination and vital rates

Additional new information on life history parameters were reviewed in SC/32/SM1, 13 and 16. No apparent correlation was seen between girth and total body length (SC/32/SM16). Females attain 50% of their adult body length by their third year, whereas males do so at approximately 5 years (SC/32/SM1). Although the mean calving month was reported to be July for Alaskan white whales, Braham reported that recent sightings suggest that the calving period was from mid-April through September (SC/32/PS10). The sub-committee restates its request to continue analysis on ageing techniques, specifically using teeth, so as to allow more refined estimates of age-related reproductive parameters.

4.2.1.3 Estimates of net reproductive rates

No new estimates of mortality using empirical data were submitted this year, but additional information was provided on birth rates (% calves as a proportion of all other animals observed) and gross recruitment (% pregnancies × % females in the population). Birth rate in the Quebec population (SC/32/SM16) was calculated at 8%, which translates into a gross recruitment of 11–14%. From a review of the literature, Brodie (SC/32/SM17) calculated that net recruitment (rate) should be 7.5%, assuming a 12% birth rate and 4.5% mortality rate. No additional new information was received on density-dependent change in rates of production; this issue remains unresolved.

4.2.1.4 Commercial and subsistence takes

The recent catch of white whales for Canada and Denmark are reported in Table 2. Boulva (SC/32/SM5) presents data which may provide some insight into the quality of reported data on whales landed. For the northern Quebec and Hudson Bay area, reported catches were less than the estimated catches by 11–27%, with an increasing trend since 1976. Breton – Provencher (SC/32/SM16) estimates that the rate of exploitation for the Poste-de-la-Baleine area of southwest Hudson Bay is 8–13%, which would exceed maximum sustainable exploitation limit for this population.

The same can be said for the Cumberland Sound population where Brodie (SC/32/SM17) showed that net production nearly equals the quota. A catch quota of 40 animals has been initiated beginning in 1980, which is mutually agreed upon by the Canadian Government and Inuk hunters. Educational pamphlets such as that by Brodie (1972) represent a useful management tool.

The subsistence take for Alaska populations are reported in SC/32/SM13. This represents an average removal (1968–79) of 184 animals from a population which is perhaps in excess of 5,000 (SC/31/SM8 and 13) or 3–4%. In Cumberland Sound 10–13%, using an average of 82 animals per year, were removed between 1972 and 1979 (SC/32/SM17 and 16). Stock separation along the Alaskan coast has not been investigated, something the sub-committee urgently requests be addressed.

Removals from the White and Kara Seas were not reported, but from SC/32/SM1 a minimum of 266 were reported killed. Whether these were part of a subsistence take or for scientific purposes was not specified. Catch statistics from Soviet waters are urgently requested, as well as an evaluation of effort and loss rate, particularly for the Sea of Okhotsk and adjacent coast of the Soviet Union Far East and Chukchi Sea area.

Hunting loss rate

Few data were provided on loss rates. In shallow water, loss rates in the Alaskan take were estimated at 20%, but in deeper water about 60% (SC/32/SM13). This means that the annual removal in Alaska, where as much as one third of the take is in deep water, may exceed 300 animals. These data provide better estimates than the undocumented ones presented last year, but this problem is an important issue for small stocks which are being harvested, or for those stocks for which we have no reliable population size estimates. Additional loss rate values were addressed by Sergeant in a minority opinion report at last year's meeting (*Rep. int. Whal. Commn* 30: 122). Brodie recorded a minority view of loss rates in Appendix 3 to this report.

The sub-committee recommends that research be initiated on killed-but-lost and wounded-but-lost rates so that greater confidence can be placed on the significance of annual removals. For example, if a 20–33% loss rate is occurring (which may be too high an estimate—Appendix 3) for the Cumberland Sound population, and all or some of these whales die, then the total take may equal or exceed the estimated net recruitment (SC/32/SM17). Such research should also examine alternative hunting techniques which might reduce losses, particularly for those populations where significant removals are now occurring.

4.2.1.5 MSY and status of stocks

Estimates of MSY for white whale stocks are not possible. Breton – Provencher (SC/32/SM16) states that the exploitation rate for the Poste-de-la-Baleine population is estimated at 13%. The actual removal rate was calculated at 9.5% (38 animals removed from a population estimated at 400). This population and the Cumberland Sound population are being exploited near or beyond their net reproductive rate. Research is especially needed on gross recruitment. It is recommended that calf counts be conducted on the Cumberland Sound population.

For all stocks, clearly better data are needed to determine recruitment rates, current exploitation rates and population levels. This is a point of great concern to the sub-committee and one needing urgent attention by all nations taking white whales.

4.3 Narwhal

4.3.1 Definition of stocks

The sub-committee reviewed the four available documents on distribution and catch from 1974 to 1979 (SC/32/SM11; SC/32/O 16; SC/32/ProgReps Canada and Denmark). From an extensive review of the literature, Mitchell and Reeves (SC/32/O 16) provisionally concluded that one stock of narwhal exists in the Canadian Arctic, West Greenland and Northwest Greenland, as opposed to two as described in *Rep. int. Whal Commn* 30: 121. They pointed out that although it is well known that narwhals in summer concentrate in separate regions of eastern Arctic Canada and north Greenland, their winter distribution is poorly known, and animals from all parts of the summer range may mix in winter in an area of Davis Strait close to the border of the drift ice. Meldgaard and Kapel (SC/32/SM11) reported recent sightings of narwhals in the Melville Bay area and reviewed previous observations from the same area. They concluded that although the catch statistics for Upunavik District clearly demonstrate a northward migration in April–June and a southward migration in September–November, it is not clear whether all these animals migrate to and from the well known summering areas in Thule District (Vibe 1950, cited in SC/32/SM11), or if some of them spend the entire summer in Melville Bay. The sub-committee was not able to agree on the question of whether one or two stocks of narwhal exists along western Greenland and near eastern Canada. This question needs further investigation, and the sub-committee recommends that the involved nations conduct such field studies as are possible to help resolve this problem.

4.3.1 Life history parameters

No new information was presented on life history, *per se*. From data reported in SC/32/ProgRep Canada however, a 23% calf-to-adult and juvenile ratio was obtained from 108 narwhals landed out of a total of 115 (4 were lost) trapped in a *savssat*. Greater numbers of females than males were in this group, suggesting that, if the entrapment was not selective, sex segregation in high latitudes may occur at this time of year.

4.3.3 Catches

The available information on recent catches is presented in Table 2 and in SC/32/ProgRep Denmark. The actual take may be more than reported (SC/32/SM11; SC/32/ProgRep Canada and SC/32/ProgRep Denmark). A review of the history of narwhal catches prior to 1930 (SC/32/O 16 suggests that the take in Canada has always been large and between 1910 and 1930 may have been as high as 400 animals per year. This is greater than the estimated take for the same period in West Greenland of over 300 per year (SC/32/O 16). Data prior to 1910 are greatly fragmented, but some were summarized by the authors. No additional data were presented on struck and lost rates, but Mitchell and Reeves (SC/32/O 16) used a value of 2 in extrapolating to total takes from the literature between 1910–30.

4.3.4 MSY and status of stocks

No estimates of sustainable yield were available; however, evidence presented in SC/32/O 16 suggests that the population has sustained a consistently high take for

Table 2

Available catch data for white whales and narwhals by area in Canada 1974–79
(From SC/32/ProgRep Canada and SC/32/O 16)

	White whales					Narwhals		
	Arctic		Hudson Bay					
Year	Eastern	Western	Eastern	Western	Totals	Eastern Arctic	Western Hudson Bay	Totals
1974	239	165	366	—	770	152	—	152
1975	140	184	529	101	954	264	7	271
1976	239	154	489	146	1,028	297	8	305
1977	286	148	534	191	1,159	200	8	208
1978	161	127	217	118	623	275	4	279
1979	200	144	1	105	450[1]	289	30	319
Totals	1,265	922	2,136	661	4,984	1,477	57	1,534

[1] 1979 data incomplete.

several centuries. A minimum population size in 1910 was estimated at 11,000 (SC/32/O 16), but no conclusions were reached on the present size of the Canadian Arctic – West Greenland stocks(s). However, Sergeant (SC/31/SM6) reported a population estimate from the recent literature of 20,000 for narwhals in the Lancaster Sound area. Although the population has sustained a long history of commercial and subsistence hunting, the sub-committee reiterates its recommendation of 1979 that additional steps be taken to obtain data on life history, distribution, abundance and other information for assessment and management of the stocks.

4.4 Other species

4.4.1 China

Chen informed the sub-committee that the *beiji* (white flag dolphin) *Lipotes vexillifer,* has been completely protected since 1975 and that no fishing for that dolphin exists at present. Historical data were reported (SC/32/SM15) detailing how the Chinese have recognized and described *Lipotes vexillifer* for more than two thousand years. Additional information is given on the distribution of *Lipotes*. Most noteworthy is that the dolphin was never common in Lake Dogtinghu (formerly transliterated as 'Tung Ting Lake') and now has entirely disappeared from the lake, due to silting. Its range at present is restricted to the middle and lower reaches of the Changjian (formerly 'Yangtse') River, and the population is much reduced. A review was provided of research on the species since the 1970s. It was also noted that a *Lipotes* Research Group was established at the Institute of Hydrobiology, Wuhan, People's Republic of China nearly two years ago. The research programme includes the following topics: (1) ecology, (2) morphology, anatomy and histology of the respiratory system, and (3) transportation and rearing of animals. One live dolphin was captured on 11 January 1980 by fishermen of Jiayu County, Hubei province and it was successfully transported live back to the Institute of Hydrobiology and is still alive at the time of our meeting. The sub-committee thanked Chen for this important new information and looks forward to hearing about the results of the studies as they progress.

4.4.2 Japan

In addition to the directed takes listed in IWS (Prov. LXXXV), local fisheries in Japan took another 13,868 small cetaceans, of 12 species (SC/32/ProgRep Japan and Appendix 4), for a total of 13,899. This includes incidental takes and the Iki Island takes. As noted above (3.2), Ohsumi reported that a planned research programme on small cetaceans described last year (*Rep. int. Whal. Commn* 30: 128) has not yet been launched. The sub-committee is concerned about the lack of research on the identity, size and status of stocks of these species under exploitation.

4.4.3 Denmark

In addition to the directed take listed in IWS (Prov. LXXXV) for the Faroes and that summarized above for Greenland, Greenland in 1979 took 960 small cetaceans, of 3 species (SC/32/ProgRep Denmark).

4.4.4 Indonesia

An open-boat whale fishery of long standing still exists in Lamalera, Lembata, eastern Indonesia and takes small cetaceans of several species (SC/32/ProgRep Australia and SC/32/O 10.

5. PROBLEMS OF INTERACTIONS BETWEEN FISHERIES AND SMALL CETACEANS

In 1978, (*Rep. int. Whal. Commn* 29: 26–7) the Commission endorsed the recommendations of the Scientific Committee that research by member nations should be encouraged into competition between small cetaceans and fishermen and that statistics and data on all types of small cetacean fisheries (including direct, incidental and live-capture) should be submitted to the IWC as part of the national progress report. The sub-committee had before it the following progress reports containing material related to this subject: SC/32/Prog Reps Canada, Denmark, Japan, Norway, South Africa, USA and the USSR. The sub-committee also reviewed the following documents containing material relevant to this subject: SC/32/SM6, SC/32/SM8, SC/32/O 5 and Kasuya and Izumizawa, 1980 (draft contract report prepared for US Marine Mammal Commission). Additional information was provided by sub-committee members and invited experts.

5.1 Incidental takes

5.1.1 Canada

SC/32/ProgRep Canada contained detailed information on cetaceans entrapped in fishing gear during 1979. The reported mortality of small cetaceans is much less than that for humpback, fin and minke whales. Gear involved included salmon nets, traps, gillnets, and seal nets. It is understood that research on measures to reduce entanglement and death of large cetaceans from entanglement is being undertaken by the Canadian government. The sub-committee urges that the research continue and that, if possible, a report be made available to the next meeting.

5.1.2 US

SC/32/O 5 contains records of the incidental catches on the US East Coast during the period 1975–79 of 12 small cetaceans taken incidentally in fishing gear. In addition 16,682 dolphins are estimated to have been taken in the US tuna purse-seine fishery in the eastern tropical Pacific (see 5.1.8).

5.1.3 South America

Valdivia reported that in 1979, the Institute del Mar del Peru (IMARPE) had been unable to carry out investigations into small cetaceans. He has reported now that no additional information is available on incidental takes of dolphins in Peruvian purse-seining operations.

5.1.4 West Africa

G. T. Sakagawa of the Southwest Fisheries Center, La Jolla, California attended the 1st Special Meeting of the International Commission for the Conservation of Atlantic Tunas (ICCAT) in November 1979 as IWC observer. His report was available as IWC/32/11B. In the Standing Committee on Research and Statistics (SCRS) of ICCAT, documentation on whale and dolphin involvement in tuna purse-seine fisheries in the eastern Atlantic was presented. 0–4% of sets were made on dolphin-associated schools and a larger percentage on whale-associated schools. A report by Levenez, Fonteneau and Regalado (SRCS/79/105) compares observations on fleet logs from January 1976 and

June 1979. 30 captains were interviewed and estimated sets on dolphin-associated schools as about 10 per cent per vessel, approximately 3% of sets for those vessels setting on dolphins at all. Log-book analysis substantiates the estimate of 0–4% of all sets for those vessels examined, about 70–80% of tuna seiners fishing in the area. Captains estimate that about 15 dolphins are killed in each set on dolphin-associated tuna.

5.1.5 South Africa

SC/32/ProgRep South Africa contains details of 104 entanglements and 100 deaths of dolphins in shark nets of Natal. The kill is the highest recorded since collection of statistics began in 1972. Although dolphins are killed in nets in all months of the year, 69% of the mortality occurred in an eleven-day period during an exceptionally large run of sardine.

Measures taken to minimise the catch of dolphins include furling nets ahead of the sardine run. In half of the cases where dolphins were killed in the 1979 run, nets had not yet been rolled up.

5.1.6 Japan

SC/32/ProgRep Japan provides data on both incidental and directed takes of small cetaceans. Directed takes are considered above (3.4.4). Incidental takes occur in fixed net, purse-seine and drift-net fisheries and totalled 1,008, of 10 species.

5.1.7 China

SC/32/SM 15 provides detailed information on the beiji, *Lipotes vexillifer*. Examination of 100 individuals killed between 1950 and 1980 indicated that 50 were killed as a result of ingesting hooked fish.

The sub-committee expressed concern that continued high mortality attributable to interaction with line fisheries continues to seriously threaten the remaining population.

5.1.8 Eastern Tropical Pacific (purse-seining for tuna)

Incidental takes from US vessels are subject to the provision of the US Marine Mammal Act of 1972, under which permits for incidental takes in the tuna industry have been issued since 1974. In 1976 a mandatory observer programme was initiated. US import regulations require that tuna taken in association with dolphins by vessels of other countries for export to the United States are also taken in accordance with the provisions of the US Marine Mammal Act. Allen (SC/32/SM6) reported on tuna purse seine operations.

In 1976 the Inter-American Tropical Tuna Commission (IATTC) recognised that it had a responsibility to concern itself with the problem of dolphin mortality associated with the purse-seine fishery, and an international observer scheme was in operation for the first time in 1979. Observers placed on board IATTC member and non-member vessels have given reports for seiners from Canada (2), Costa Rica (2), Mexico (1), Nicaragua (1), Panama (4) and the USA (111). Sets on dolphins in the Eastern Tropical Pacific were also made by seiners from Congo, Costa Rica, Ecuador, South Korea, Mexico, Netherlands Antilles, New Zealand, Nicaragua, Panama, Senegal, Spain, the USA and Venezuela. Estimates of mortality have been made for all known sets (SC/32/SM 6). Total estimated mortality of all species in estimated at 23,595. The species involved are spotted dolphin, spinner dolphin, common dolphin, striped dolphin and bottlenose dolphin. These estimates for 1979 are the first that have been presented for the entire Eastern Tropical Pacific yellowfin purse-seine fishery.

The incidental takes by the US are closely regulated, with catch limits set for each known stock of each species based on assessments of status. For some stocks, for example the eastern spinner dolphin, the current catch limit is zero. Provisional quotas for 1980 total 31,150.

The sub-committee noted that reports on tuna-fishery associated incidental takes of small cetaceans had not been submitted by several IWC members (United Kingdom—Bermuda tuna purse-seine activities—and Cayman Islands, Peru and Spain).

5.2 Direct conflicts and competition

5.2.1 Japan

Catch information was available to the sub-committee in a draft report to the US Marine Mammal Commission (Kasuya and Izumizawa, draft report, 1980) on the drive fishery at Iki Island. Catches for 1979 are in Appendix 4. The figures here are those reported by the Katsumoto Fish Co-op Union.

A research team established by the Japanese Agency of Science and Technology in 1978 was transferred to the Japanese Fisheries Agency in 1979 and has continued its work in 1980. In 1979, 313 of the dolphins killed were examined; in 1980, 445 of the 1,819 killed were examined.

A second proposed research programme was reported by T. Ichihara of Tokai University in an unpublished document presented to the meeting on cetacean behaviour and intelligence and the ethics of killing cetaceans, held in Washington DC in 1980. The proposal includes research on detection of sounds emitted by dolphins, to allow approaching schools to be detected; research on effects of sound on dolphins, to develop means of moving dolphins away from fishing areas; and research on reactions of fishes to sounds used to scare dolphins, to avoid additional interference with fishing.

The sub-committee urges that all efforts be made to quantify the possible competition between these small cetaceans and continued yellowtail and squid fisheries in the area to assess the effects of continued take from the small cetacean populations.

5.2.2 Australia

Anderson reported that in September 1979, reports were received that a small number of killer whales were taking hooked fish in a dropline fishery which is developing off the east coast of Tasmania. Fishermen reported losses of 30% of daily catches. Fish were taken from droplines by the whales as the lines were being winched aboard. The interference was having a serious local impact on the fishery, and on some days boats remained in port to avoid what was considered as continued harassment. No action was taken, pending information on methods used for dispersal of cetaceans in other fisheries. Fishing resumed uninterrupted when the possible single pod of whales moved off.

Anderson reported that it is intended to undertake a more detailed examination of the fishery during 1980 and to monitor the behaviour of killer whales in the area should the interaction re-occur. Non-injurious methods of dispersal, including aversive conditioning, may also be assessed and will be fully reported at the next meeting.

5.2.3 Norway

A fishery for killer whales in Norwegian coastal waters has been carried out in part as a measure against perceived interference in the herring fishery. Data and further comment on the fishery is contained above in discussion under item 4.1.2.

6. EFFECTS OF POLLUTION AND INDUSTRIAL DEVELOPMENT

6.1 New information on pollution

6.1.1 Mercury levels

SC/32/SM16 reported mercury levels in white whales in the Poste-de-la-Baleine region, New Quebec. Tissue samples from 22 animals were examined.

It appears that between the ages of 0–27 dentinal growth layer groups, mercury concentrates eight times more rapidly in liver than in muscle, rising from 0.4 to about 12 ppm in liver and from 0.14 to 1.5 ppm in muscle. In practical terms, the livers of animals longer than 2.44 m and the meat of animals longer than 2.75 m are not fit for human consumption. Large animals are hunted, but as the hunters eat only the 'Muktuk' (skin) they avoid the risk of ingesting excessive amounts of mercury.

SC/32/O 11 analysed meat samples from a number of species, including short-finned pilot whales and killer whales. The former showed a range of 10.7 to 64.2 ppm, mean 26.2 ppm wet weight. The samples, however, are described as 'semi-dried' and had a moisture content of only 26.7%. the single killer whale sample, described as fresh, had a moisture content of 71% and 15.6 ppm wet weight of mercury.

As the aim of this study was to assess mercury levels in meat samples as consumed by humans, the disparate nature of the samples may perhaps be overlooked. It should be noted, however, that these levels are almost certainly not representative of those in fresh caught material and that the possibility that the samples had been contaminated before purchase was not explored. The quoted Japanese standard of 0.4 ppm refers to fish, but is similar to the Canadian standard mentioned in the previous paragraph. Further discussion of this paper may be found in the Scientific Committee Report, item 13.1.

6.1.2 Organochlorine pollutants

A study by O'Shea, *et al.,* (in press) of organochlorine pollutants in small cetaceans from the Pacific and South Atlantic Oceans was noted. The abstract was available to the sub-committee and an early draft had been seen by some members. Sixty-nine individuals representing 10 species were sampled. Collections were made from 1968 to 1976 in the eastern tropical Pacific and along the coasts of California, Hawaii, Japan and Uruguay. Total DDT and PCB residues in blubber of most of the 19 individuals of the five southern California species sampled exceeded concentrations which are associated with reproductive impairment in pinnipeds, although the nature of such associations is not well defined. Only one individual, a rough-toothed dolphin from Maui, Hawaii was not contaminated. Details of the reproductive condition of the animals were not included in the paper but are available from the authors.

Brodie pointed out the importance of recording the sex of animals in studies of pollutants. He stated that in grey seals, for example, both sexes accumulate DDT at the same rate until sexual maturity. After this, the males continue to accumulate DDT, but in females, pregnancy and lactation seem to act as a sink.

In view of the lack of information on the exact relationship between high concentrations of organochlorides and reproductive impairment, particularly in marine mammals, future studies should endeavour to include anatomical and histological studies of reproductive tissue.

6.1.3 Other information

Kapel, reporting on a joint session of the ICES Marine Mammal Committee and Environmental Quality Committee, said that while there was much evidence on the levels of pollutants in the tissues of marine mammals, there was little information about the physiological effects of these contaminants.

He further reported that some studies have been completed and others are underway. The local populations of fish and marine mammals are known to be contaminated with metal and pesticides. Cadmium, for example has been found in large quantities in ringed seals. It is possible that this metal is more severely damaging than mercury. The situation is further complicated by possible interactions between different types of residues, particularly mercury and selenium. The next joint meeting will be held in the first week of October 1980.

The Inland Sea in Japan has a pollution problem, but Kasuya and Kureha (1979) recently reported that sightings in the area reveal a considerable stock of finless porpoise. While information on previous population levels is not available, nevertheless this does show that even in a highly polluted area it is possible to find a considerable stock of small cetaceans.

The sub-committee notes and emphasizes that the majority of studies only dealt with the amounts of pollutants and not with their effects. Some members felt that the sub-committee should not be concerned about pollution, as there is no evidence that the accumulation of pollutants have affected the physiology or stock status of cetaceans. Other members thought that as other animals were known to be damaged, it is important to continue to investigate the problem, although such studies are difficult, not least because captive animals are known in some instances to react differently than wild animals to these substances. It is also important that studies include anatomical and histological investigations so that possible confounding effects of infections, etc., may be made clear.

Studies of PCB and other pollutants' effects in small cetaceans and dugongs are being carried out by N. Miyazaki at the National Science Museum, Tokyo. Arima and Nagakura (1979) have published a study of mercury and selenium in odontocetes.

The review by Risebrough (1979) on pollutants in marine mammals was noted, as was the information that in the United Kingdom the Royal Commission on Environment Pollution is investigating the effects of oil pollution on marine biota, including marine mammals. Braham reported that studies of effects of oil on cetaceans are presently being conducted by US Scientists; they will be reported on at next year's meeting.

6.2 New information on industrial development

6.2.1 China

SC/32/SM15 noted that among the factors causing the decline of the *Lipotes vexillifer* population are destruction of the habitats due to harnessing the river and increasing navigation. Chen further remarked that individuals apparently killed by propellors showed wounds only on the head. These were extensive, with the skull opened or partly cut away. No body wounds were seen.

6.2.2 Baffin Bay and Davis Strait

SC/32/ProgRep Denmark states that the possible effects of a Canadian project for transportation of liquified natural gas (LNG) along the West Greenland coast on stocks of marine mammals in Baffin Bay and Davis Strait and their exploitation by local people have been reviewed. Kapel reported that the matter is still under review. The project, which has not yet been approved, would begin in 1986 at the earliest. Gas has been found in northern Canada and the problem is to transport it to consumers to the south. The proposed 'Arctic Pilot project' includes construction of two very large transport ships (340 m in length and 200,000 horsepower) which would be able to sail on a year-round basis. 60 passages a year (about one every six days) are planned. The suggested route would pass very close to the Greenland coast, and the plan has caused much concern in Greenland. This is mainly on two grounds: one, that this activity may interfere directly with hunting; and two, that it may also affect the stocks of marine mammals and birds breeding or migrating through the area. Of special concern is that the noise from such ships is of an order of magnitude not previously known in this area. Kapel reported that a Danish specialist has calculated that cavitation noise from the ships will dominate ambient noise and have a masking effect on marine-mammal echo-location for more than 100 km on each side of the passage. Cetaceans are known to use sound for echo-location and/or for communication, and it is not known to what extent this new noise will affect the animals.

A working group has been set up with scientists and representatives from the Greenland and Canadian governments and representatives of the Canadian Crown Corporation concerned. Two or three meetings have taken place to identify the problems and to determine what research is needed. A priority is to design a route which will do least damage to marine life.

In further discussion of the High Arctic, it was pointed out (SC/32/O 16), and the sub-committee agreed, that in view of (1) the extensive development underway or planned in the Canadian Arctic; (2) the dependence of the narwhal on a deep-basin High Arctic habitat; (3) the likelihood that Canadian narwhals may all belong to a single stock and the only one 'sufficiently large and concentrated to ensure species survival', a larger research effort than currently exists should be carried out to investigate scientifically the possible and probable impacts on the narwhal habitat and population of proposed developments in the Davis Strait, Baffin Bay and Lancaster Sound regions.

7. OTHER BUSINESS

7.1 Review of CITES report

The Scientific Committee requested that members of the sub-committee review the small-cetacean portions of a draft of an expanded and revised version of 'Proposals Concerning the Cetacea'. The members of the sub-committee agreed that time would not allow review of the document during the meeting. Several members agreed to review the draft and forward comments to Klinowska.

7.2 Meeting on cetacean reproduction

The sub-committee recognises the continuing need for a special meeting (with a laboratory-based workshop component) on cetacean reproduction as it relates to stock assessment and management, emphasizing reproduction in female odontocetes. An invitation and offer of partial funding have been received by the Commission from the Southwest Fisheries Center. The tentative date would be the first week in December, 1981. The sub-committee members find the place and time suitable and recommend that the invitation be accepted.

8. RECOMMENDATIONS TO THE SCIENTIFIC COMMITTEE

8.1 Northern bottlenose whale

The sub-committee recommends that the research programme recommended for the northern bottlenose whale in 1977–78 be carried out and that the stock continue to be classified a Protection Stock with a zero catch.

8.2 Killer whale

The sub-committee recognises that the IWC has a mandate to classify killer whale stocks (the killer whale is listed in the IWC Schedule, Section I, paragraph 1), and to set catch limits for them. Thus, the sub-committee is recommending appropriate stock classifications as well as research that it believes is necessary.

(1) Noting that until 1979/80 the catches of killer whales have been a small fraction of the estimated stock size for a part of the waters near Antarctica, the sub-committee recommends that the stock(s) be classified as an Initial Mangement Stock. Because it has not been able to perform an adequate stock assessment for this area, the sub-committee is unable to recommend a catch limit on scientific grounds.

(2) Noting a lack of information about reproductive rates, natural mortality rates, stock structure, and the effects of various harvesting regimes on social structure, the sub-committee recommends that the USSR be asked to continue its research with the aim of providing adequate data for stock assessments. The sub-committee also recommends that the USSR be made aware of the requirement for collecting full catch and biological statistics for *each* killer whale taken by catcher vessels (Schedule VI.24).

(3) Noting that the Norwegian exploitation of killer whales in the North Atlantic has a long history of catches, the sub-committee recommends that this stock be provisionally classified as a Sustained Management Stock, with a catch limit of 54 pending an assessment of the population. The provisional classification would require review at next year's meeting.

(4) Noting that no estimates of population size are available for the killer whales in Norwegian coastal waters, the sub-committee recommends that Norway be asked to conduct research to provide this and other information necessary for an adequate stock assessment.

(5) Noting that the management criteria used by the Commission do not address situations where the interest of another marine resource has an impact on whale management, such as may be the case for the Norwegian exploitation of killer whales, the sub-committee recommends that the Commission be requested to instruct the Scientific Committee on suitable management critera for such situations.

(6) Recognising that there is much field research in progress on killer whales, in North America, South America, the USSR and elsewhere, and that much of the existing relevant expertise has not been available to the sub-committee in its efforts to assess killer whale stocks, the sub-committee recommends that a three- or four-day workshop on stock identity and population structure of killer whales be convened before the next meeting of the Scientific Committee.

8.3 White whales and narwhals

Recommendations on white whales and narwhals made last year to the Commission by the Scientific Committee were not acted upon, pending a legal review of the status of IWC *vis a vis* cetaceans not presently listed in the Schedule. The sub-committee therefore reiterates the substance of recommendations, taking into account new information available at this meeting.

(1) The sub-committee believes that management of the aboriginal/subsistence fisheries for white whales and narwhals should be considered by the Commission in the same manner as is the bowhead fishery in the Bering Sea and Arctic Ocean. White whales of some stocks and narwhals on the one hand and bowhead whales on the other both undergo long migrations, crossing national territorial boundaries. Both are taken by indigenous peoples using light craft and harpoons, with various modifications derived from modern technology. The only substantive differences between the fisheries are in size of the whales and the size and organisation of the whaling crews involved, differences not justifying the radically different treatment presently given them. The sub-committee recommends to the Committee that the white whale (*Delphinapterus leucas*) and the narwhal (*Monodon monoceros*) be defined as 'whales' and listed in Paragraph 1 of the Schedule thus:

> 'white whale' (*Delphinapterus leucas*) means any whale known as white whale, beluga, belukha
> 'narwhal' (*Monodon monoceros*) means any whale known as narwhal, sea unicorn

so that the appropriate management procedures may be discussed and implemented.

(2) The sub-committee recognises that for the first time a catch limit (40) has been set by the Canadian government for the Cumberland Sound stock of white whales, but because the population has declined to approximately 10–15% of its initial size, the sub-committee still must recommend on biological grounds that the stock be classified as a Protection Stock and a catch limit of zero placed on it. The sub-committee further recommends that current research on the Cumberland Sound stock of white whales be continued and expanded. The research should include regular censuses of the summering population and estimates of gross recruitment. The inter-relationships of Cumberland Sound and Hudson Strait stocks should continue to be examined. Full data on age, sex, size and reproductive status should be obtained from the catch, should there be one.

(3) The sub-committee noted that the white whales that winter along the southern coast of West Greenland and at the edge of the pack ice migrate to summering areas in the central Canadian High Arctic and in the Melville Bay – Thule areas on Greenland. Although catches in Greenland have been of 400–1,500 animals annually for over 100 years and no population estimate is available for the latter summering groups, the sub-committee believes it possible that current levels of removals are too high for the overall population. The sub-committee recommends that these groups, which winter in south-west Greenland waters, be provisionally managed as one stock and that Canada and Denmark (Greenland) be urged to initiate a joint research program on this stock(s). Of particular importance is an accurate census of the numbers of white whales summering in Melville Bay – Thule District and Canadian and Greenland waters of Smith Sound and Kane Basin and analysis of inter-relationships among these and adjacent summer populations. The program should also include more accurate determintion of the killed-but-lost rates associated with the various types of hunts in Greenland and Canada.

(4) The sub-committee believes the catch levels for white whales that inhabit the Barents, White, Kara and Laptev Seas are substantially above even annual gross production or that the present population estimates are incomplete. The new information made available at this meeting did not include abundance estimates. The sub-committee, therefore, recommends that the USSR be urged to commission a study of the components of the Barents Sea wintering group and an assessment of the stock or stocks involved.

(5) The main wintering grounds and composition of the Bering Sea group of white whales are largely unknown, and sizes and inter-relationships of the summering groups are also poorly known, including those in Soviet waters. Although present removals from these groups may be sustainable, it is probable that harvests will increase as indigenous populations increase or alternative subsistence needs arise. For example, the white whale is one alternative to the bowhead. The sub-committee therefore recommends that national research programs be instituted by the USA, USSR and Canada. These programs should begin soon and should include documentation of loss rates, characteristics of the hunt and collection of biological samples for determination of vital parameters. The temporal and spatial components of the populations should be determined, the populations censused and the relationships among them identified.

8.4 Competition with fisheries

The sub-committee considers that while cases of perceived competition for common resources between fisheries interests and cetacean populations are reported from many areas, there is as yet no case in which quantitative verification is available. The sub-committee therefore again recommends that member nations be urged to foster and support expanded research on perceived competitive interactions between marine mammals and fishermen. The sub-committee strongly urges that such perceived competition be assessed in direct quantitative terms.

8.5 Pollution

The sub-committee is particularly concerned about the lack of knowledge concerning the short- and long-term effects of pollution on cetaceans and recommends that member nations be especially urged to investigate the physiological effects of pollutants on growth, reproduction and mortality.

8.6 Terminology

(1) The sub-committee recommends that the Bureau of International Whaling Statistics be requested in

compiling IWS to follow the list of common and scientific names accepted by IWC as a convention (*Rep. int. Whal. Commn* 27: 25 and Appendix 1). The list has not been followed in past issues of IWS. For example in Vol. LXXXIII of IWS the following corrections are needed:

(a) Common porpoise reported caught in the USA in Table Z^2 are actually common dolphins, *Delphinus delphis*.

(b) Northern bottlenose whales, *Hyperoodon ampullatus*, reported caught by the USSR in Table Z^4 are southern bottlenose whales, *H. Planifrons*.

(c) Long-finned pilot whales, *Globicephala melaena*, reported caught by Japan and the British West Indies in Table Z^5 are short-finned pilot whales, *G. macrorhynchus*.

(d) Common porpoises reported caught by the USA in Table Z^{10} are common dolphins, *Delphinus delphis*.

(2) The sub-committee recommends that the common name *beiji* be substituted for *white flag dolphin* (an erroneous translation of the Chinese name) for *Lipotes vexillifer* in the IWC List of Small Cetaceans recognised (*Rep. int. Whal. Commn* 27: 483).

8.7 Statistics

As discussed above, statistics supplied by member nations for directed and incidental takes of small cetaceans are in very many cases incomplete or inadequately detailed. The sub-committee again recommends that member nations again be requested to collect and submit full statistics, as detailed in last year's recommendation (*Rep. int. Whal. Commn* 30: 124).

8.8 Tuna-seining in the eastern tropical Pacific

The sub-committee recommends that member nations purse-seining for tuna associated with dolphins in the eastern tropical Pacific, or planning to do so, be urged to participate in the international observer programme operated by the Inter-American Tropical Tuna Commission. These nations at present include the United Kingdom (Cayman Islands and Bermuda), Peru and Spain.

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Appendix 1

AGENDA

1. Participants, agenda and introductory remarks.
2. Review of documents.
3. Review of management actions and research on northern bottlenose whale, striped dolphin, Dall's porpoise and harbour porpoise.
4. Other directed fisheries on small cetaceans.
   - 4.1 Killer whale.
   - 4.2 White whale and narwhal.
   - 4.3 Narwhal.
   - 4.4 Other species.
5. Problems of interactions between fisheries and small cetaceans.
   - 5.1 Incidental takes.
   - 5.2 Direct conflicts and competition.
6. Effects of pollution and industrial development.
7. Other business.
8. Recommendations to the Scientific Committee.

Appendix 2

ABUNDANCE ESTIMATES FOR KILLER WHALES IN ANTARCTIC AREAS III AND IV

R. Allen

Best (SC/32/SM10) estimated the abundance of killer whales using line transect methods with a negative exponential distribution of sighting distances. Although a chi-squared test did not reveal differences between the observed and fitted distributions, there is a clear discrepancy in the first interval. In fact the chi-squared test does not have very much power in distinguishing between observed and fitted curves, particularly when only a small number of degrees of freedom are available. Furthermore, for line transect estimation it is critical that the fitted distribution of sighting distances fits the observed distribution well at the origin.

To attempt to overcome this a truncated negative binomial distribution (Best and Butterworth, 1980, *Rep. int. Whal. Commn* 30: 257–83) with a cut off point at 0.5 miles was fitted to the data given in SC/32/SM10. In the original analysis the parameter for the negative exponential distribution was estimated from the data as a whole, and then the lengths of track line, areas, and number of observations were stratified into 9 areas. This was done in an attempt to remove the effects of non-homogeneous densities through the area. However, the effect of estimating the parameter of the distribution from the pooled data and population estimates from stratified data is unknown, and this analysis is done for the combined data. Although line-transect theory assumes the population density is homogeneous for unbiased estimates from an area within a non-homogeneous one, it is sufficient that track lines be random with respect to areas of high and low density.

Appendix Table 1

Frequency distribution of right and sighting distances for killer whales with fits to the negative exponential distribution truncated at 0.5 miles and to the untruncated negative exponential distribution (SC/32/SM 10)

Distance interval n miles	Observed frequency	Truncated negative exponential	Negative exponential
0–0.1	14	13	9
01–0.2	8	9	8
02–0.3	6	6	7
03–0.4	4	3	6
04–0.5	2	3	5
	34	34	29

Appendix Fig. 1 shows the sampling effort (length of track line/area) plotted against relative density (numbers sighted/length of track line) for the eight strata with observations. This graph shows that although there is a considerable amount of scatter, there was in fact relatively more sampling in high density areas than in low-density areas, and thus an estimate made without stratification is likely to be an over-estimate of the true population.

With a cut off point of 0.5 months, the data extracted from SC/32/SM10 (excluding the stratum with no observations) were:

$n = 34$ numbers of schools seen.
$A = 960{,}484$ area surveyed.
$L = 14{,}239$ length of track line.

Then the estimate of λ using

$$\lambda = \frac{n-1}{\Sigma y}\left(1 - \frac{0.5\lambda e^{-\lambda/2}}{1-e^{-\lambda/2}}\right)$$

was 3.94, and the estimate of N, the total number of schools in the area, using

$$\hat{N} = \frac{nA}{2L}\;\frac{\lambda}{1-e^{-\lambda/2}}$$

was 5,250. Appendix Table 1 shows the fequency distributions of right angle distances for the observations and fits to the truncated and untruncated distributions.

The average school size given in SC/32/SM10 was 11.66, and thus the estimate of population size is 61,200. This is a little more than double the estimate given in SC/32/SM 10 and the difference is more or less equally due to the difference between using a truncated and non-truncated model and to the difference between the partial stratification and pooled methods. It is clear from Fig. 1 of this Appendix that pooling will lead to some over-estimation of numbers but it is also likely that the partial stratification introduces a bias. The use of the truncated model will produce a better estimate of the density than the untruncated one, providing the relatively large observation in the zero-to-0.09 n miles category is not an artefact caused by whales actively moving towards the boat.

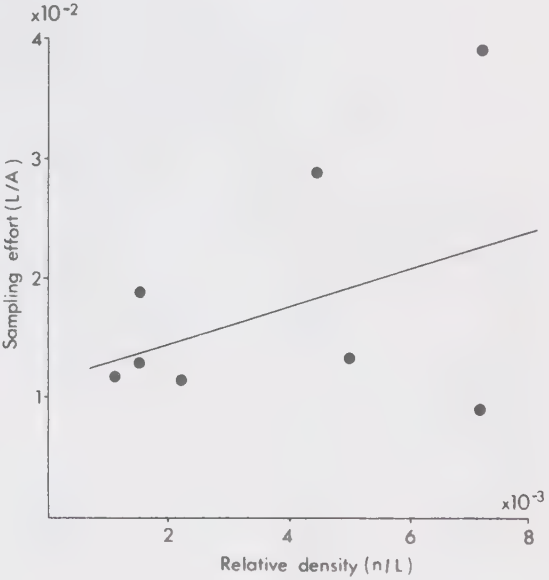


Fig. 1. Regression of sampling effort on relative density (see text).

The coefficient of variation estimated using the negative exponential distribution was 0.25. The coefficient of variation for the truncated model used here is difficult to calculate and consequently the coefficient of variation for the ordinary model is used for a rough guide to the statistical variation in the estimates. Because a part of the variance is the result of random variation in n which is common to both estimates this is likely to be an over-estimate. If it is assumed that the estimates are symmetrically distributed an approximate 95% confidence interval would (30,600, 91,800).

Appendix 3

HUNTING LOSS RATE FOR WHITE WHALES IN CANADA

P. Brodie

A single percentage-loss rate cannot be applied for all hunting activities across the Canadian Arctic. Loss rates are not only site specific but hunter specific.

The skills of the hunter and the type of rifle used are further complicated by the salinity and turbidity of the water. For example, the Mackenzie delta hunting area is of low salinity and high silt load. Whales are easily lost due to lower buoyancy and once lost cannot be seen through the muddy water. In addition, wounded animals would have increased wound infection due to the lower salinity.

Heavier-calibre rifles used in the Mackenzie delta tend to cause greater wounds (observed by Brodie in 1972) than in the Canadian Eastern Arctic.

The Cumberland Sound hunting is generally with lighter, high velocity rifles (for seal hunting) which tend to cause more superficial wounds. The higher salinity not only reduces the sinking but provides better healing conditions for escaping wounded animals.

Effective strategies are used by hunters, such as driving animals into shallow water before killing them or harpooning before the killing shot.

Appendix 4

CATCH OF SMALL CETACEANS IN 1979 BY SPECIES AND COUNTRIES

(D = Direct, I = Incidental, and L = Live capture)
(1 Provisonal, 2 1979/80 Antarctic Season, 3 Estimated total, and 4 Non-USA Kill in Eastern Tropical Pacific)

		Japan	Canada	Denmark		Norway	USSR	South Africa	USA	Non-USA^{4}	Total
				Greenland	Faroes						
Baird's beaked whale	(D)	28	—	—	—	—	—	—	—		28
Northern bottlenose whale	(I)		1	—	—	—	—	—	—		1
Narwhal	(D)		319	350^{3}	—	—	—	—	—		669
	(I)		1								1
White whale	(D)		449^{1}	700^{3}	—	—	—	—	—		1,149
	(I)		2	—	—	—	—	—	—		2
Indo-Pacific hump-backed dolphin	(I)		—	—	—	—	—	1	—		1
Melon-headed whale	(D)	140	—	—	—	—	—	—	—		140
False killer whale	(D)	339	—	—	—	—	—	—	—		339
Killer whale	(D)	5	—	—	—	221	916^{2}	—	—		1,142
Long-finned pilot whale	(D)	—	—	50	1,725	—	—	—	—		1,775
	(I)	—	5	—	—	—	—	—	—		5
Short-finned pilot whale	(D)	93	—	—	—	—	—	—	—		93
	(I)	11	—	—	—	—	—	—	—		11
Atlantic white-sided dolphin	(D)	—	—	8	—	—	—	—	—		8
	(I)	—	—	—	—	—	—	—	1		1
Dusky dolphin	(I)	—	—	—	—	—	—	1	—		1
Pacific white-sided dolphin	(D)	360	—	—	—	—	—	—	—		360
	(I)	64	—	—	—	—	—	—	—		64
Bottlenose dolphin	(D)	615	—	—	—	—	—	—	—		615
	(I)	51	—	—	—	—	—	8	9^{3}		68
	(L)							4			4
Risso's dolphin	(D)	934	—	—	—	—	—	—	—		934
	(I)	1	—	—	—	—	—	—	—		1
Spotted dolphin	(D)	427	—	—	—	—	—	—	—		427
	(I)	—	—	—	—	—	—	—	8,317^{3}	3,401	11,718
Spinner dolphin	(I)	—	—	—	—	—	—	—	3,085^{3}	408	3,493
Striped dolphin	(D)	2,193	—	—	—	—	—	—	—	—	2,193
	(I)	22	—	—	—	—	—	10	321^{3}	281	634
Common dolphin	(D)	50	—	—	—	—	—	—	—		50
	(I)	39	—	—	—	—	—	23	4,950^{3}	2,421	7,433^{3}
Harbour porpoise	(D)	—	—	900^{3}	—	—	—	—	—		900
	(I)	3	—	—	—	—	—	—	7		10
Dall's porpoise	(D)	6,872	—	—	—	—	—	—	—		6,872
	(I)	828	—	—	—	—	—	—	—		828
Finless porpoise	(I)	1	—	—	—	—	—	—	—		1
Other	(D)	49	—	2	—	—	—	—	—		51
	(I)	1	1	—	—	—	—	62	—		64
Total		13,126	778	2,010	1,725	221	916	109	16,690	6,511	42,086

8152

STENELLA CLYMENE, A REDISCOVERED TROPICAL DOLPHIN OF THE ATLANTIC

W. F. PERRIN, E. D. MITCHELL, J. G. MEAD, D. K. CALDWELL, AND
P. J. H. VAN BREE

ABSTRACT.—*Stenella clymene* has not been recognized as a valid species in recent lists of cetaceans. Examination of new material allows the redescription of this valid species. Externally, it closely resembles *S. longirostris*; cranially, it resembles *S. coeruleoalba* in shape, but is smaller. *S. clymene* shares many features with these two species and is probably closely related to both of them. *S. clymene* is now known from New Jersey, Florida (both coasts), Texas, the Caribbean, the mid-Atlantic and West Africa. New records of *S. longirostris* extend its known range in the western Atlantic north to Cape Hatteras and south to Rio de Janeiro.

Gray (1846) described *Stenella clymene* (as *Delphinus metis*) from a single skull from an unknown locality. This nominal species was subsequently placed in the synonymies of other species or considered separately, and its habitat and external appearance have remained unknown. On the basis of examination of new material, we have determined that the species is valid, that it inhabits the tropical Atlantic and that it is closely related to *S. longirostris*, the spinner dolphin.

We first suspected that *S. clymene* is a valid species in 1975, when one of us (WFP) noted resemblance of the skulls of two dolphins from the Texas Gulf Coast to the holotype of *S. clymene* in the British Museum. Photographs of the Texas dolphins showed them to have coloration similar to that of the spinner dolphin, *S. longirostris*. In shape, the skull of *S. clymene* closely resembles that of the striped dolphin, *S. coeruleoalba*. This discordant resemblance of the skull of *S. clymene* to that of one species and the external appearance to that of another perhaps accounts for the longstanding uncertainty concerning the existence of the species. The new material has made possible for the first time examination of adequate suites of external and skeletal data from the same specimens.

MATERIALS AND METHODS

Varying combinations of skeletal, external, and photographic data were available for 71 specimens of spinner dolphins or spinner dolphin-like specimens from the Atlantic. The holotypes of *S. clymene* and *S. longirostris*, from unknown localities, and an additional skull from an unknown locality but labeled *S. clymene* were examined. Of the total of 74, 19 were judged to be *S. clymene* and 55 were assigned to *S. longirostris*. In addition, 21 skulls of *S. coeruleoalba* from the Atlantic and two holotypes of species in the synonymy of *S. coeruleoalba* but from unknown localities were measured, and additional measurements of skulls of that species were extracted from the literature (True, 1889; Busnel et al., 1968; van Bree et al., 1969; Robineau, 1972) and, for some of the specimens listed below, from unpublished notes by F. C. Fraser.

Measurements of skeletal characters were made as described by Perrin (1975). External measurements follow the Committee on Marine Mammals (American Society of Mammalogists, 1961). Distal fusion of premaxillaries and maxillaries was used as the criterion of adulthood for inclusion of skulls in adult series. Specimens were adjudged physically mature (for inclusion in adult series of postcranial skeletons) if all vertebral epiphyses were fused to the centra.

We examined 17 of the 31 specimens of *S. coeruleoalba* for distal fusion of the premaxillaries and maxillaries. Only 6 (with condylobasal lengths of 435, 436, 442, 460, 465, and 491 mm) exhibited fusion. To increase the sample size we included an additional 12 skulls ≥ 435 mm long (CB = 435–466), of which 6 (CB = 436–457) were known juveniles and 6 were of undetermined age. The holotype of *S. coeruleoalba* (ZMB 51226) was destroyed during World War II. The holotype, although possessing the color pattern definitive of this species, was a juvenile (CB = 403, no distal fusion evident in figure published by True, 1889).

J. Mamm., 62(3):583–598, 1981

Specimens included.—Specimens of *S. clymene* are listed in the redescription of that species. Full names of institutions are included in Acknowledgments.

Stenella longirostris.—U.S. ATLANTIC COAST: Cape Hatteras, North Carolina, 2 (USNM 291352, 504524; 291352 may have been collected in the former fishery for bottlenose dolphins, *Tursiops truncatus*, at Cape Hatteras—Mead, 1975); Bulls Island, South Carolina, 1 (USNM 500859); Mayport, Florida, 2 (R-3-SLS, R-4-SLS: in possession of DKC); Miami, Florida, 1 (University of Miami, Department of Zoology, unnumbered). GULF OF MEXICO: Casey Key, Florida, 25 (USNM 504433–504456, 504460); Dog Island, Florida, 3 (USNM 504223, 504224; UF 7861); Fort Walton, Florida, 1 (LSUMZ 17017); Sabine Pass, Texas, 1 (TCWC 28286); Padre Island, Texas, 3 (TCWC 29035 and 2 unnumbered for which skeletal specimens were not saved). CARIBBEAN: Cuba, 1 (STV #1, only photo seen); St. Vincent, Lesser Antilles, 6 (SV-1-SL, SV-2-SL, SV-3-SL, SV-4-SL, SV-5-SL, SV-6-SL; in possession of DKC); Venezuela, 1 (ZMA 15.138). WEST AFRICA: Vridi, Ivory Coast, 1 (USNM 470557); Liberia, 1 (RMNH 21.720); Senegal, 5 (ZMA 12.263, 13.146; 13.147, IFAN no. 2; EDM 784). UNKNOWN LOCALITY: 1 (RMNH 8676: the holotype of *S. longirostris*).

Stenella coeruleoalba.—MEDITERRANEAN: France, 1 (MNHN A3021: the holotype of *Delphinus tethyos* Gervais 1853). EASTERN NORTH ATLANTIC: Cornwall, England, 2 (BMNH SW19341, 1940.3.2.1); N. Devon, England, 1 (BMNH 1938.2.5.1); 44°00′N latitude, 28°24′W longitude, 1 (EDM 758). WESTERN NORTH ATLANTIC: Massachusetts, 2 (USNM 20877, MCZ 51763); New York, 2 (USNM 504086, 504261); 37°42′N latitude, 73°34′W longitude, 1 (MCZ 50406); 37°10′N latitude, 74°00′W longitude, 1 (MCZ 51708); Virginia, 1 (USNM 504859); North Carolina, 4 (USNM 504134, 504761, 504880, and 504885); 37°28′N latitude, 72°09′W longitude, 1 (EDM 798). CARIBBEAN: St. Vincent, Lesser Antilles, 1 (SV-78-1-SC, in possession of DKC). WESTERN SOUTH ATLANTIC: Rio de la Plata, 1 (ZMB 51226: the holotype of *Delphinus coeruleoalbus* Meyen 1833). UNKNOWN LOCALITIES IN ATLANTIC: 2 (UZMC no. 18 and UZMC no. 1). UNKNOWN LOCALITIES: 2 (BMNH 1861.4.2.7: the holotype of *Tursio dorcides* Gray 1866; BMNH 1920.5.13.1: the holotype of *Delphinus euphrosyne* Gray 1846).

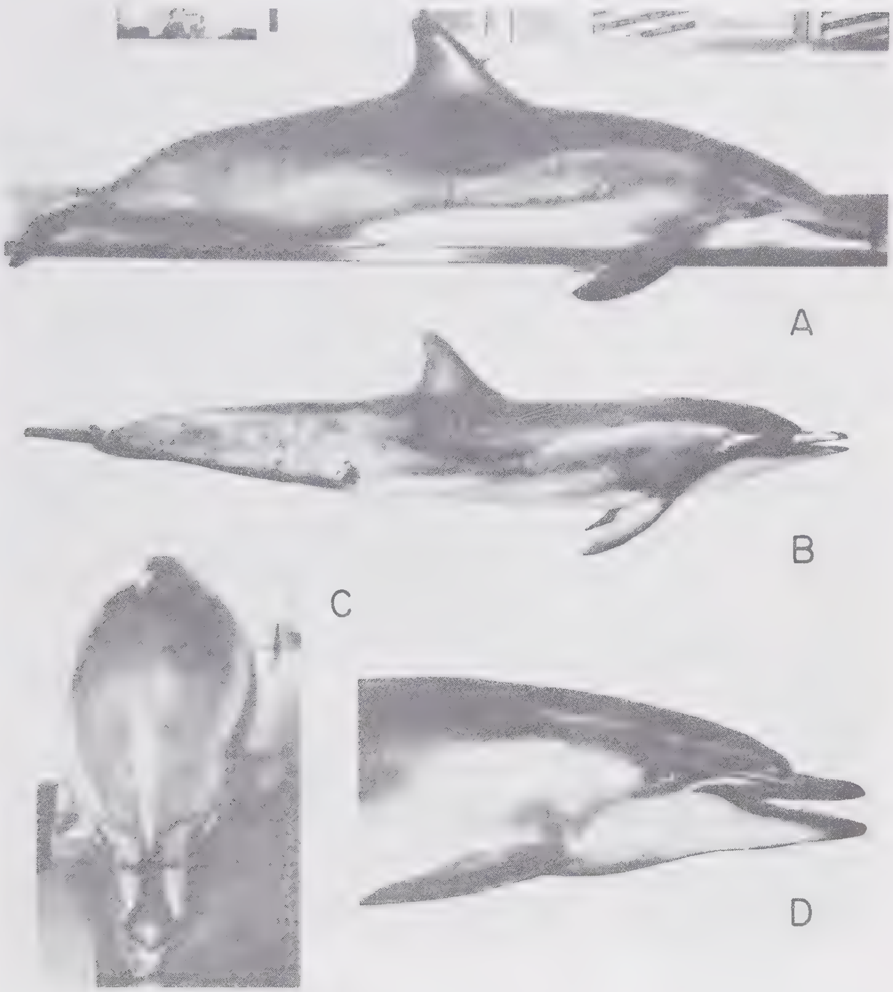
Redescription of **Stenella clymene**

1846. *Delphinus metis* Gray [no. 2], Zoology of the voyage of H.M.S. *Erebus* and *Terror*, 1 (Mammalia): 39 (not pl. 18; not *Delphinus metis* Gray, 1846:38 = *Tursiops truncatus*).
1850. *Delphinus clymene* Gray, Cat. Mamm. British Mus., Cetacea, p. 115 (replacement name for *D. metis* Gray 1846:39, preoccupied by *D. metis* Gray 1846:38).
1866. *Clymene normalis* Gray, Proc. Zool. Soc. London, 1866 (a):214.
1868. *Clymenia normalis*, Gray, Synopsis whales and dolphins, British Mus., p. 6.
1884. *Delphinus clymene*, Flower, Proc. Zool. Soc. London, 1883:498.
1898. [*Prodelphinus*] *clymene*, Trouessart, Cat. Mamm., p. 1036.
[*Prodelphinus*] *normalis*, Trouessart, Cat. Mamm., p. 1036.
1966. *Stenella clymene*, Hershkovitz, Bull. U.S. Natl. Mus., 246:26.

Holotype and type locality.—Adult skull, British Museum of Natural History (BMNH) no. 350a, no accompanying data.

Distribution.—Tropical and subtropical Atlantic. Not known to occur in Indian or Pacific oceans. This is unusual for a tropical cetacean. Perrin et al. (1978) noted the possible existence of endemic tropical dolphins in the Atlantic and speculated that they may represent forms that arose during Pleistocene isolation of the warm Atlantic from the Indopacific.

Diagnosis.—The color pattern of *S. clymene* (Figs. 1 and 2) differs from the very similar pattern of *S. longirostris* as follows: the ventral margin of the cape below the dorsal fin dips toward the ventral margin of the lateral field (terminology of Perrin, 1969, 1972), whereas in *S. longirostris* the two margins are parallel for most of the length of the animal; the upper and lower margins of the flipper stripe converge markedly as they approach the eye, whereas in *S. longirostris* they are all but parallel; and the black tip of the beak is bordered dorsally with a distinctive pale-gray-to-white



(USNM 504408); (B) lateral view of Curacao specimen (AMNH 239115—suspended vertically from rope around flukes), and (D) lateral view of anterior portion of Florida specimen (R-1-SLS).

blaze, instead of with the pale-to-dark-gray field that is adjacent to the black tip in *S. longirostris.* The blaze interrupts the black gape border distally, just behind the black beak tip, heightening the visual impact of the blaze. The eye stripe in most delphinids, including most specimens of *S. longirostris*, extends forward to the apex of the melon. At about one-third of the distance from melon apex to beak tip, the line zig-zags several times before merging with the black dorso-mesial mark that includes the beak tip, yielding a variable "moustache mark" in dorsal view. The blowhole stripe (from blowhole to apex of melon) is approximately the width of the blowhole and is composed of pale bordering lines enclosing a slightly darker-gray area and a faint pale-gray mesial line, yielding an overall impression of a pale stripe shading aburptly into the black mesial mark of the beak.

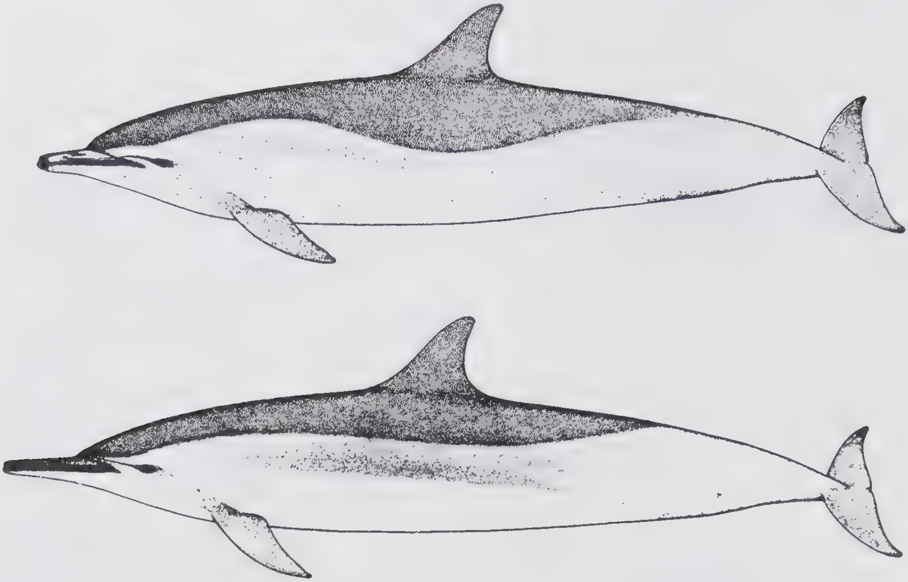


FIG. 2.—Color patterns of *Stenella clymene* (top, drawn from photographs of USNM 504408, R-1-SLS, and AMNH 239115) and *S. longirostris* (bottom, drawn from photographs of several specimens).

External measurements for 10 specimens are in Table 1. Six adult specimens ranged from 183 to 196 cm long. Two of these were physically mature and were 184 and 186 cm long. The beak is relatively short, 9–11 cm long in the 8 adult specimens for which this measurement was taken.

Adult skulls of *S. clymene* can be separated from the skulls of the closely related *S. longirostris* and *S. coeruleoalba* by their relative length and breadth (Figs. 3 and 4).

Comparisons.—The color pattern (Figs. 1 and 2) resembles that described by Perrin (1972) for *S. longirostris* in Hawaiian waters, a pattern also typical for that species in the Atlantic (Leatherwood et al., 1976). Points of close correspondence are a three-part pattern consisting of dark-gray cape, pale-gray lateral field, and white ventral field; a dip in the ventral margin of the cape over the eye; flipper stripe from flipper to eye and bordered above by a pale stripe; pale gular region; and a system of black markings that border the gape, cover the tip of the beak, and extend posteriorly along the midline of the beak to the apex of the melon, whence it continues as a pale stripe posteriorly to the blowhole. These features separate *S. clymene* and *S. longirostris* from the other beaked dolphins, including *S. attenuata/frontalis* (nomenclature unsettled—IWC, 1975), *S. plagiodon*, *S. coeruleoalba*, *Delphinus delphis*, *Tursiops truncatus*, *Lagenodelphis hosei*, *Lagenorhynchus* spp., and *Steno bredanensis*. The white ventral field in *S. clymene*, as in some specimens of *S. longirostris*, is flecked with very small irregular dark spots. The spots are most numerous near the border of the lateral gray field.

The beak is shorter than in adult specimens of *S. longirostris* (Table 2). *S. clymene* also has relatively small flippers, on the average about 2 cm shorter and 1 cm narrower than in *S. longirostris*. Although the sample sizes are small, *S. clymene* also may have a smaller dorsal fin and greater axillary girth than does *S. longirostris*.

TABLE 1.—*Selected external measurements of 10 specimens of* Stenella clymene. *Estimates are in parentheses.*

	UZMC Lütken #7	UZMC Lütken #9	UZMC Lütken #13	IFAN (no no.)	AMNH 239115	Caldwell R-1-SLS	USNM 504408	UF14186	UF14187	UF14188
Sex	F	M?	M		F	M	M	M	M	M
Adult?	(No)	(Yes)	(Yes)		Yes	Yes	Yes	(Yes)	(Yes)	(Yes)
Physically mature?					No	Yes	Yes			
Total length (cm)	168	177	185	183	188	184	186	196	187	184
Tip of upper jaw to:										
apex of melon		9		10	11	10	10	11	11	11
center of blowhole	31	29	32	31	27	29	29	28	32	32
center of eye	29		33	30	30	28	28		(~32)	
end of gape				26	26	24	24	26	28	27
ant. insertion of flipper	43		48		45	40	42	44	43	44
umbilical scar					92	87	89			
center of genital slit					134	118	121	123	116	118
center of anus					139	133	137	142	131	133
Girth at axilla					85	95	93			
Girth at anus	56		62		56	66	68			
Ant. length of flipper		22*		29	28	28	28	28	29	22*
Width of flipper		8		8	9	8	9	9	9	8
Width of flukes		43			47	48	46	(~43)	(~46)	(~45)
Height of dorsal fin				29*	16	20	16	18	18	
Weight (kg)				58	68.2		85.8			
Measurements by:	From Lütken (1889); long measurements may not have been taken parallel to body axis.			From Cadenat and Doutre (1958)	EDM	DKC	JGM	R. S. Wells	R. S. Wells	R. S. Wells

* Apparently anomalous due to measuring technique.

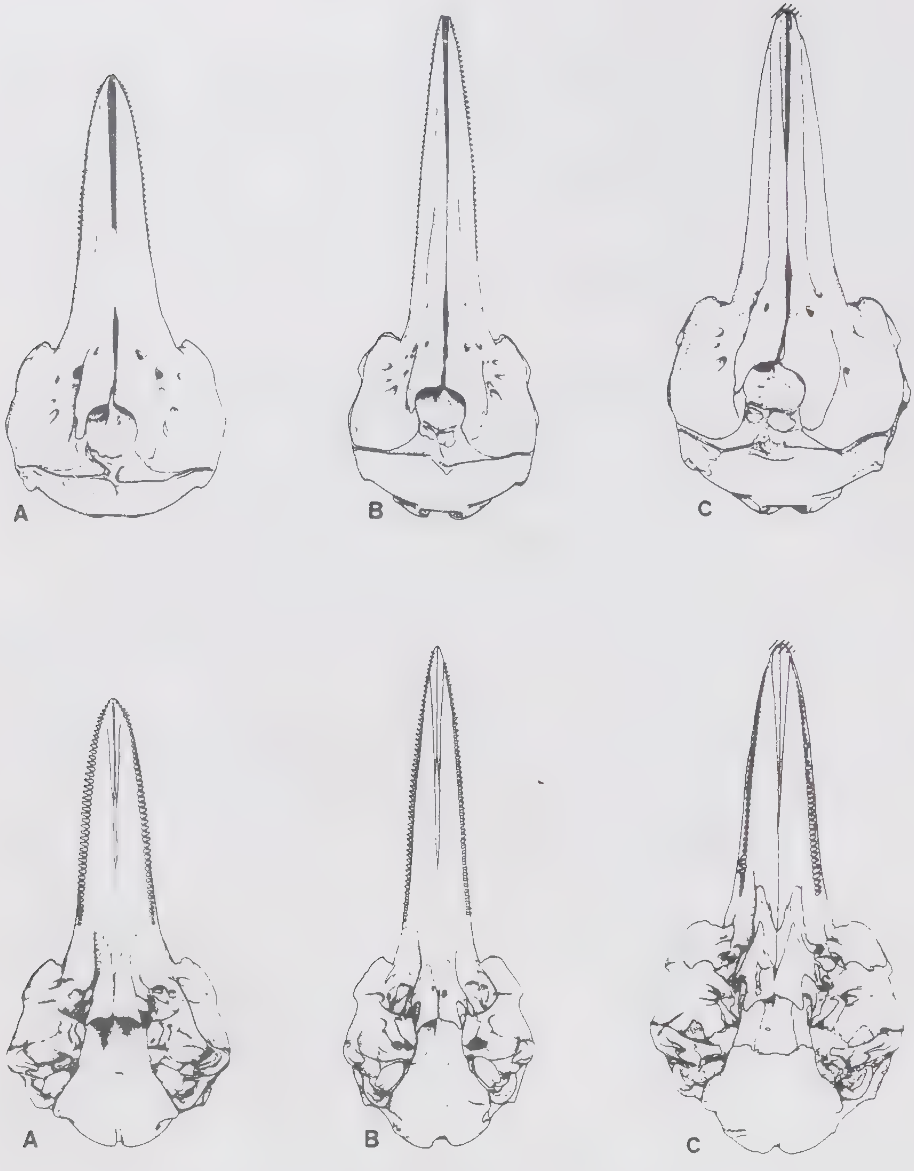


FIG. 3.—Comparison of skulls of *Stenella clymene* (A, drawn from R-1-SLS, physically mature male, CB length = 392—broken teeth have been restored in the drawing), *S. longirostris* (B, drawn from R-3-SLS, sexually mature female, CB length = 437 mm), and *S. coeruleoalba* (C, drawn from USNM 504885, male, CB length = 436 mm, ≈5 mm missing rostrum tip restored and cross hatched).

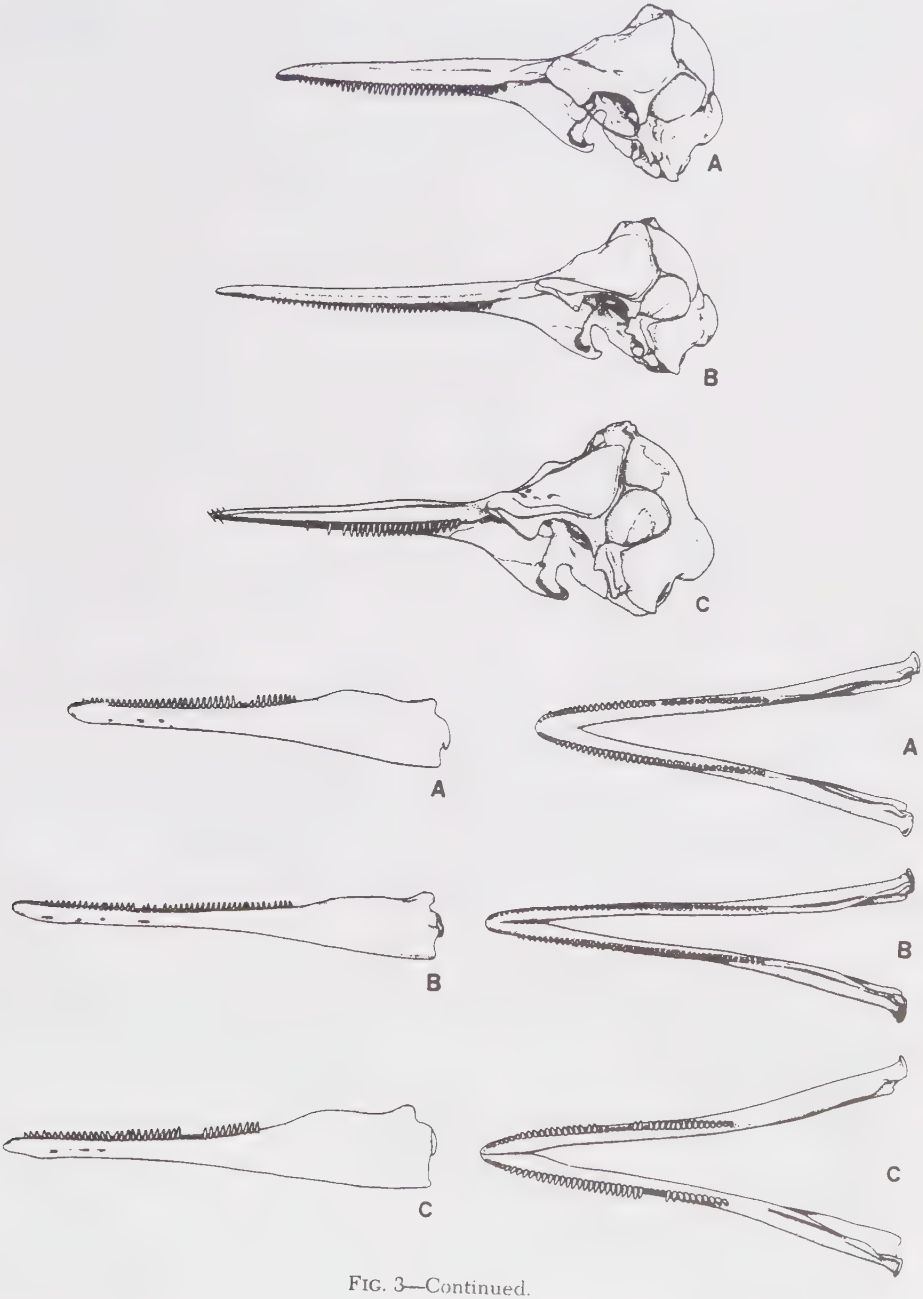


FIG. 3—Continued.

TABLE 2.—*Means, standard deviations (for sample sizes >30), sample sizes (in parentheses), and extremes for selected external measurements (in cm) of adult specimens of* Stenella clymene *and* S. longirostris. *Males and females considered separately for measurements found by Perrin (1975) to vary by sex in* S. longirostris.

	Stenella clymene			*S. longirostris*		
	Males		Females	Males		Females
Total length	185.6 (7) 177–196*		188 (1)	192.5 (17) 173–208**		188.9 (17) 177–204***
Tip of upper jaw to:						
apex of melon	10.3 (6) 9–11		11 (1)	17.0 (16) 13–19		17.9 (16) 16–20
center of blowhole (M&F)		29.8 (8) 28–32			33.3 ± 2.11 (35) 30–39	
center of eye (M&F)		29.8 (4) 28–33			33.4 ± 1.54 (34) 30–36	
end of gape (M&F)		25.8 (6) 24–28			29.5 ± 1.93 (35) 25–33	
anterior insertion of flipper (M&F)		43.7 (7) 40–45			47.1 ± 2.42 (35) 41–53	
umbilical scar (M&F)		89.3 (3) 87–92			93.9 (23) 85–101	
center of genital slit	119.2 (5) 116–123		134 (1)	24.6 (13) 112–135		133.0 (14) 125–149
center of anus	135.2 (5) 131–142		139 (1)	142.0 (13) 128–151		135.3 (3) 130–142
Girth at axilla	94.0 (2) 93–95		85 (1)	85.9 (13) 78–94		85.2 (14) 80–98
Girth at anus	65.3 (3) 62–68		56 (1)	65.2 (12) 52–95		57.3 (14) 48–98
Anterior length of flipper (M&F)		26.8 (8) 22–29			28.9 ± 2.38 (34) 25–38	
Width of flipper (M&F)		8.5 (8) 8–9			9.6 ± 0.77 (34) 8–11	
Width of flukes	45.7 (3) 43–48		47 (1)	45.4 (16) 40–53		41.3 (17) 36–48
Height of dorsal fin	18.0 (4) 16–20		16 (1)	19.3 (17) 15–25		18.0 (17) 16–20

* Two physically mature were 184 and 186 cm long.
** Four physically mature were 192–208 cm long.
*** Two physically mature were 196 and 201 cm long.

The skull of *S. clymene* (Fig. 3, Table 3) shares a complex of features with several other small pelagic delphinids with dorsal fin and externally well-defined beak (*S. longirostris, S. coeruleoalba, Delphinus delphis,* and *Lagenodelphis hosei*): 1) a relatively small temporal fossa (reflecting a small temporal muscle); 2) a relatively large number (typically more than 40 in each row) of small, slender teeth; 3) poorly developed alveoli in the distal 1 cm or so of upper and lower jaws in most specimens; 4) proximal halves of upper and lower toothrows parallel or nearly so; 5) a relatively short mandibular symphysis; 6) distal half of the rostrum markedly flattened dorsoventrally; and 7) a grooved palate (grooves nearly absent in some specimens of *S. longirostris* and *S. coeruleoalba*). In all of these features *S. clymene* is unlike the other small pelagic (or partially pelagic) delphinids with dorsal fin and externally well-defined beak (*S. attenuata/frontalis* complex, *S. plagiodon*, and *Tursiops truncatus*).

In comparison with *S. longirostris*, the skull of *S. clymene* is relatively short and broad. The present series of specimens of the two species do not overlap in length of the rostrum, preorbital width, postorbital width, and length of the upper toothrow (Table 3). In some measurements, however, particularly those of the internal nares,

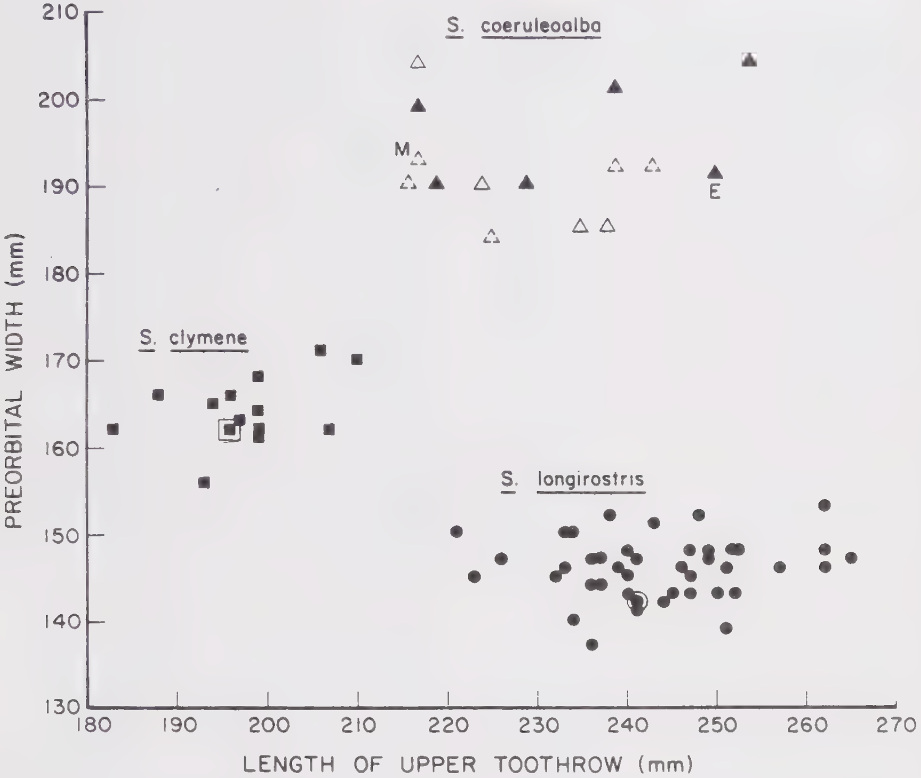


FIG. 4.—Scatterplot of preorbital width of the skull against length of the upper toothrow for 17 specimens of *Stenella clymene*, 12 of *S. coeruleoalba*, and 40 of *S. longirostris*. For *S. coeruleoalba*, solid triangles are known adults (see text), line triangles are near-adult, and dashed triangles are of unknown status. E is the holotype of *Delphinus euphrosyne* Gray, 1846, and M is the holotype of *D. marginatus* Pucheran 1868. Enclosed symbols are holotype of *S. clymene* and *S. longirostris*.

the orbit, the temporal fossa, and the brain case, there is little or no difference between the two species.

F. C. Fraser of the British Museum was the first to note the similarity of the skull of *S. clymene* to that of *S. coeruleoalba* (unpublished notes given to WFP in June 1973). He also recognized that the skull of *S. clymene* is smaller than that of *S. coeruleoalba* and tentatively referred to *S. clymene* three small skulls referred by Lütken (1889) to nominal species now in the synonymy of *S. coeruleoalba* (*Prodelphinus euphrosyne* and *P. euphrosynoides*). *S. clymene* is more like *S. coeruleoalba* than like *S. longirostris* in all measurements of the skull taken as percentages of condylobasal length (Table 4). In the measurements taken as percentages of parietal width (Table 4), however, *S. clymene* is closer to *S. coeruleoalba* except for measurements of the premaxillaries, the temporal fossa, orbit, preorbital process, and internal nares. Differences among the three species in these characters are slight.

A scatterplot of preorbital width against length of the upper toothrow (Fig. 4) separates the present series of specimens of the three species and summarizes the differences between them in shape; *S. clymene* and *S. coeruleoalba* are similar in shape but different in size, whereas *S. longirostris* differs from the other two in being longer

TABLE 3.—*Means, standard deviations (for sample sizes >30), sample sizes (in parentheses), and extremes for selected skull measurements (in mm) and skull and postcranial meristics for adult specimens of* Stenella clymene, S. longirostris, *and* S. coeruleoalba,[1] *and skull measurements and tooth counts for the holotype of* S. longirostris.

	Stenella clymene	*S longirostris* from Atlantic	Holotype of *S. longirostris*	*S. coeruleoalba*
Condylobasal length	390.0 (14) 376–409	427.0 ± 13.10 (41) 395–458	426	452.4 (18) 441–491
Length of rostrum	233.0 (14) 218–250	276.8 ± 11.00 (41) 251–304	277	264.4 (18) 246–289
Width of rost. at base	89.4 (14) 80–90	75.6 ± 3.41 (42) 68–83	76	105.5 (18) 93–115
Width of rost. at ½ length	52.4 (14) 49–58	44.4 ± 2.30 (41) 41–50	48	56.6 (18) 51–66
Width of pmx's at ½ length	25.3 (14) 21–29	21.0 ± 2.32 (37) 17–32		27.7 (17) 23–32
Width of rost. at ¾ length	39.7 (14) 36–44	31.9 ± 2.63 (39) 25–39	36	42.8 (11) 36–52
Greatest preorb. width	164.1 (14) 156–171	145.6 ± 3.86 (42) 137–153	142	192.0 (16) 184–204
Greatest postorb. width	181.6 (14) 171–190	161.1 ± 4.03 (41) 152–169	159	211.3 (17) 189–225
Greatest width of ext. nares	43.6 (14) 40–48	41.8 ± 1.63 (38) 38–45		48.7 (16) 45–52
Zygomatic width	179.1 (14) 167–189	159.2 ± 3.92 (40) 150–167	156	209.3 (17) 193–225
Greatest width of pmx's	69.3 (14) 62–74	64.8 ± 2.38 (42) 60–71	58	83.8 (18) 77–93
Parietal width	140.6 (14) 135–146	130.5 ± 4.25 (41) 121–140	125	162.4 (17) 152–169
Height of braincase	94.2 (14) 88–102	93.1 ± 3.94 (38) 85–107		107.7 (11) 98–119
Int. length of braincase	106.8 (14) 99–114	106.4 ± 3.77 (37) 99–114		127.1 (11) 124–136
Length of temporal fossa	51.3 (14) 45–56	48.1 ± 3.30 (42) 42–56	50	64.6 (18) 53–72
Height of temporal fossa	39.2 (14) 32–44	38.3 ± 3.52 (42) 30–49	43	48.9 (18) 37–61
Length of orbit	46.2 (13) 44–48	41.8 ± 2.10 (39) 39–50		51.6 (11) 38–58
Length of preorb. process	46.9 (14) 43–50	43.4 ± 2.23 (39) 38–48		57.3 (11) 47–64
Width of int. nares	50.4 (14) 47–55	46.5 ± 2.26 (37) 42–53		60.3 (11) 55–69
Length of upper toothrow	198.1 (14) 183–210	243.5 ± 10.30 (41) 221–265	241	230.8 (15) 216–254
Teeth: u. (avg.)	43.6 (10) 39–49	55.4 ± 3.01 (41) 48–64	54 & 53	45.2 (26) 39–51
l. (avg.)	42.6 (10) 38–47	53.9 ± 3.32 (43) 47–62	52 & 54	44.8 (27) 39–55
Length of ramus	330.9 (13) 316–347	368.4 ± 11.68 (40) 343–399	368	386.3 (16) 367–419

TABLE 3.—*Continued.*

	Stenella clymene	*S. longirostris* from Atlantic	Holotype of *S longirostris*	*S. coeruleoalba*
Height of ramus	58.3 (13) 56–62	56.4 ± 2.28 (41) 51–61	57	68.4 (16) 64–74
Diameter of tooth (at midlength of lower row, transverse at alveolus)	2.87 (11) 2.4–3.4	2.47 (29) 2.1–3.0		3.56 (9) 3.0–4.1
Depth of palatal groove (at midlength of rostrum)	1.4 (11) 1–2	1.0 ± 0.17 (34) 1–2		0.8 (11) 0–1
Total no. of vertebrae	73.8 (6) 73–75	71.7 (27) 69–75		76.2 (9) 71–79
No. of thoracic vertebrae	14.5 (6) 14–15	14.6 (26) 13–16		14.4 (10) 13–15
No. of lumbar vertebrae	18.6 (5) 17–21	17.7 (23) 16–21		22.5 (4) 22–23
No. of caudal vertebrae	33.0 (5) 31–35	32.3 (22) 31–34		33.3 (3) 32–35

[1] Includes 29 Atlantic and Mediterranean specimens (including holotypes of *D. tethyos* Gervais 1853 and *D. marginatus* Purcheran 1856) and holotypes of *Tursio dorcides* Gray 1866 and *D. euphrosyne* Gray 1846, both from unknown localities.

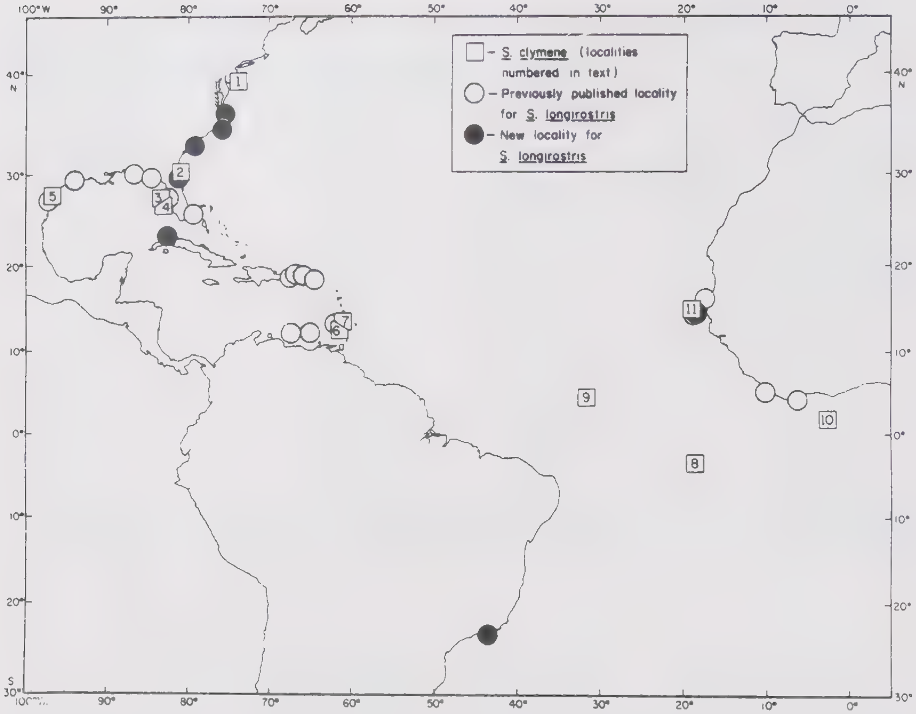
and narrower. No small juvenile skulls of *S. clymene* were available for study; they may prove difficult to separate from juvenile skulls of *S. coeruleoalba*.

Tooth counts overlap in the three species (Table 3), but *S. clymene* has about as many teeth per row (38–49) as does *S. coeruleoalba* (39–55), about 10 fewer than in *S. longirostris* (47–64). The range of within-species variation in vertebral count in the present series is smaller than that in tooth count (3–8 versus 11–16). The range for *S. clymene* (73–75, n = 6) is similar to that for *S. longirostris* (69–75, n = 27), whereas *S. coeruleoalba* may have more vertebrae (71–79, n = 9). The difference is mainly in the lumbar series (17–21 in *S. clymene*, 16–21 in *S. longirostris*, and 22–23 in *S. coeruleoalba*).

The palatal grooves that are markedly developed in *Delphinus delphis* and *Lagenodelphis hosei* are present in *S. clymene*, albeit only 1 to 2 mm deep (at half-length of the rostrum). The grooves are also present in *S. longirostris* and *S. coeruleoalba*, although in some specimens of both species they may be so weakly expressed as to all but disappear beyond about the proximal one-third of the osseous palate.

Relationships.—Of three major functional complexes definable in the delphinid skull and assessed in the present series of specimens (braincase, feeding apparatus, and breathing and sound-making apparatus), the braincase appears to be the least plastic (Perrin, 1975), the feeding apparatus the most plastic. Based on the close similarity of *S. clymene* to *S. longirostris* in some cranial dimensions and in color pattern, we suspect that *S. clymene* is more closely related to *S. longirostris* than to *S. coeruleoalba*. This implies that the similarity in skull shape to that of the externally dissimilar *S. coeruleoalba* reflects a convergence affecting mainly the feeding apparatus and the breathing and sound-making complex (the beak and the "face"), perhaps reflecting a convergence in species, size, or depth-distribution of prey and in foraging tactics.

Arnason (1980) described the C- and G-banded karyotypes of *S. clymene* and found them to be strikingly similar to those of the white-beaked dolphin, *Lagenorhynchus albirostris*, and the harbor porpoise, *Phocoena phocoena*, with chromosome number


☐ – S. clymene (localities numbered in text)
○ – Previously published locality for S. longirostris
● – New locality for S. longirostris
100°W
90°
80°
70°
60°
50°
40°
30°
20°
10°
0°
40° N
30°
20°
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S 30°
1
2
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4
5
6
7
8
9
10
11

FIG. 5.—Distribution of *S. clymene* and *S. longirostris* in the Atlantic.

of 2n = 44. He found no differences between G-banded karyotypes of *S. clymene*, *S. plagiodon*, and *Tursiops truncatus*, and only a few minor differences between their C-banded karyotypes, indicating a high degree of karyotypic conservatism in the Delphinidae.

Ecology.—*Stenella clymene* has been observed at sea only in deep water (250 to 5,000 m or deeper). It appears that it may be a midwater or night feeder on small fishes and squids. The stomach of the specimen stranded in New Jersey contained one pair of squid beaks (unidentified) and over 800 very small otoliths. The otoliths were badly eroded and could be identified only to genus or family. Myctophids predominated; there were 780 otoliths of *Ceratoscopelus* sp., seven of *Lampanyctus* spp. (at least 2 species), and seven of *Symbolophorus* sp. In addition to the myctophid remains, there were five otoliths tentatively identified as of an argentinid, one of *Bregmaceros* sp., and three unidentified otoliths. All the myctophids, except *Lampanyctus* spp. and *Bregmaceros* sp., are mesopelagic but are known to reach the surface at night during the course of vertical migrations (Perrin et al., 1973). *Lampanyctus* usually does not occur in surface waters even at night. The diet of this specimen was similar to that of *S. longirostris* in the eastern Pacific (Fitch and Brownell, 1968; Perrin et al., 1973) and *S. coeruleoalba* in the western Pacific (Miyazaki et al., 1973).

The Caribbean specimen (AMNH 239115) exhibited several well-healed circular or oval scars representing wounds that may have been made by the "cookie-cutter shark," *Isistius brasiliensis* (Jones, 1971). One animal photographed at sea had a fresh oval wound, on its back, of the type inflicted by this small pelagic shark.

TABLE 4.—*Skull proportions in* Stenella clymene, S. longirostris, *and* S. coeruleoalba *calculated as percentages of condylobasal length and of parietal width, from mean values in Table 3.*

	Percentage of condylobasal length			Percentage of parietal width		
	S. clymene	*S. longirostris*	*S. coeruleoalba*	*S. clymene*	*S. longirostris*	*S. coeruleoalba*
Condylobasal length	—	—	—	227.4	327.2	278.6
Length of rostrum	59.7	64.8	*58.4	165.7	212.1	162.8
Width of rostrum at base	22.9	17.7	*23.3	63.8	57.9	65.0
Width of rostrum at ½ length	13.4	10.4	*12.5	37.3	34.0	34.9
Width of pmx's at ½ length	6.5	4.9	*6.1	18.0	16.1	17.1
Width of rostrum at ¾ length	10.2	7.5	*9.5	28.2	24.4	26.4
Greatest preorbital width	42.1	34.1	*42.4	116.7	111.6	118.2
Greatest postorbital width	46.6	37.7	*46.7	129.2	123.5	130.1
Greatest width of external nares	11.2	9.8	*10.8	31.0	32.0	30.0
Zygomatic width	45.9	37.3	*46.3	127.4	122.0	128.9
Greatest width of premaxillaries	17.8	15.2	*18.5	49.3	50.0	51.6
Parietal width	36.1	30.6	*35.9			
Height of braincase	24.2	21.8	*23.8	67.0	71.3	66.3
Internal length of braincase	27.4	24.9	*28.1	76.0	81.5	78.4
Length of temporal fossa	13.2	11.3	*14.3	36.5	**36.9	39.8
Height of temporal fossa	10.1	9.0	*10.8	27.9	**29.4	30.1
Length of orbit	11.9	9.8	*11.4	32.9	**32.0	31.8
Length of preorbital process	12.0	10.2	*12.7	33.4	**33.3	35.3
Width of internal nares	12.9	10.9	*13.3	35.9	**35.6	37.1
Length of upper toothrow	50.8	57.0	*51.0	140.9	186.7	142.1
Length of ramus	84.9	86.3	*85.4	235.4	282.3	237.9
Height of ramus	15.0	13.2	*15.1	41.5	43.2	42.1

* *S. clymene* closer to *S. coeruleoalba* than to *S. longirostris*.
** *S. clymene* closer to *S. longirostris* than to *S. coeruleoalba*.

Behavior.—In the Caribbean, this dolphin has been observed to "spin" (R. V. Walker, pers. comm.). The spinning leaps observed, however, were not as high or complex as those exhibited by the spinner dolphin, *S. longirostris* (Hester et al., 1963). Several individuals seen in the Gulf of Guinea rode the bow wave, and the animals have approached vessels sufficiently closely on several occasions to make them vulnerable to harpooning from the bow. A school of this species was seen in the company of a large school of common dolphins, *Delphinus delphis*, off the coast of West Africa (Cadenat and Doutre, 1958).

Common name.—This dolphin has not had a vernacular name in the literature, aside from Gray's (1846) "the Clymene." We propose that it be called "the clymene dolphin."

Specimens examined and records of occurrence (numbered in Fig. 5).—U.S. ATLANTIC COAST: near Ocean City, New Jersey (Locality 1), 1 (USNM 504408); St. Augustine, Florida (Loc. 2), 3 (R-1-SLS and R-2-SLS, in possession of DKC; R-3-SLS, photograph only, in possession of DKC). GULF OF MEXICO: Sarasota Bay, Florida (Loc. 3), 3 (UF 14186–8); St. Petersburg, Florida (Loc. 4), 2 (R-G-1-SLS—photos only, in possession of DKC); Yarbrough Pass, Texas (Loc. 5), 3 (TCWC 25576, unnumbered "Hildebran's specimen," LSUMZ 18519). CARIBBEAN: near Curacao, 12°25′N latitude, 61°36′W longitude (Loc. 6), 1 (AMNH 239115); St. Vincent (Loc. 7), taken in local fisheries (R. V. Walker, pers. comm.). MID ATLANTIC: 3°40′S latitude, 18°5′W longitude (Loc. 8), 2 (UZMC Lütken no. 7 and no. 13); 4°18′N latitude, 31°20′W longitude (Loc. 9), 1 (UZMC Lütken no. 9). WEST AFRICA: Senegal (Loc. 11), 1 (IFAN, no number; photo and external measurements only, in Cadenat and Doutre, 1958); Gulf of Guinea, 2°10′ N latitude, 2°30′W longitude (Loc. 10; photos only, one in Leatherwood et al., 1976, under *S. longirostris*).

ATLANTIC: 1 (UZMC Lütken, no. 12). UNKNOWN LOCALITIES: 2 (BMNH 350a, the holotype of *S. clymene*, and BMNH 1947.7.2.2).

The St. Augustine and St. Petersburg specimens were referred by Caldwell and Caldwell (1975) to "*Stenella longirostris* sensu lato." Schmidly et al. (1972) identified the Texas specimens as *Stenella frontalis*, and Schmidly and Melcher (1974*a* and 1974*b*) repeated that identification. Based on Perrin et al. (1977), Schmidly and Shane (1978) later applied the name *S. clymene*.

Distribution of S. longirostris

Perrin (1975) summarized published records through 1972. Additional published records since then include those in Erdman et al. (1973), Lowery (1974), Dupuy and Maigret (1976), Taruski and Winn (1976), Shane (1977), Schmidly and Shane (1978), and Mead et al. (1980). The limits of the known range of the species in the western Atlantic have been extended over 600 km north (from Miami, Florida, to Cape Hatteras, North Carolina) and some 2,100 km south (from Venezuela to southern Brazil; Fig. 5). In addition to the previously unpublished records included in the list of specimens examined, we have two more sighting records. (1) On several occasions in November 1979, G. N. di Sciara (pers. comm.) observed and photographed large groups (150–400) of spinner dolphins near Isla Margarita, Venezuela. (2) Motion-picture footage taken off Rio de Janeiro, Brazil, by researchers at Instituto de Pesca, Sao Paulo, and seen by one of us (WFP), shows several spinner dolphins riding the bow wave of a vessel. This is the southernmost record of the species for the Atlantic. As noted by Brownell and Praderi (1976), although this tropical dolphin could be expected to occur throughout the tropical Atlantic, previous "records" from the South Atlantic have been unsubstantiated.

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L. A. Zavala Camin, Instituto de Pesca, Santos, Brazil, allowed us to include his unpublished record of *S. longirostris* off Rio de Janeiro, and G. N. di Sciara, Hubbs-Sea World Research Institute, San Diego, California, allowed us to include his records from off Venezuela. J. E. Fitch identified the fish otoliths from the New Jersey specimen of *S. clymene*. K. S. Raymond drafted the figures. D. W. Rice, R. L. Brownell, Jr., W. E. Schevill, R. V. Walker, G. T. Sakagawa, and I. Barrett read the manuscript and offered suggestions for its improvement.

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ESTIMATION OF THE AGE OF A TROPICAL REEF FISH USING THE DENSITY OF DAILY GROWTH INCREMENTS

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ABSTRACT

Daily growth increments found in the otoliths of *Pristipomoides filamentosus* (Pisces: Lutjanidae) were used to estimate the ages of the larger and older individuals which are harvested in the commercial deep-sea handline fishery in Hawaii. Previous investigations have been limited to visual counts of all rings present in an otolith, precluding the possibility of aging large fish. A method was devised in which the density of increments within an otolith is related to fish size and age is estimated by regression statistics.

To date 81 otoliths have been analyzed from fish ranging in size from 18 to 70 cm fork length. Sagittae were read from the focus to the antirostral margin of the otolith in frontal sections. Numerous determinations of the density of daily increments were made at measured distances from the focus by microscopic examination and statistical regressions were performed on these data. Integration of the regression equation, bounded by the focus and the otolith margin, provides an estimate of the age in days of the sample specimen. Independent size-frequency data confirm the daily periodicity of the increments.

Overall, approximately 77% of the variation in increment density was explained by the linear model. Error estimates of age were obtained by the Delta Method, a propagation of error technique. In general, the coefficient of variation for age estimates is about 6%, indicating an acceptable level of precision. This new method of obtaining age estimates may prove valuable in the management of tropical fish stocks if assumptions concerning growth interruptions and increment periodicity can be satisfied.

INTRODUCTION

Within the last decade, studies of fish otolith microstructure have revealed the startling fact that these calcified structures often grow by daily accretion of increments. Pannella (1971, 1974) was the first to demonstrate this and others have substantiated his findings for a wide variety of temperate and tropical species in both marine and freshwater environments (Brothers et al. 1976, Le Guen 1976, Struhsaker and Uchiyama 1976, Ralston 1977, Taubert and Coble 1977, Barkman 1978, Methot and Kramer 1979, Wild and Foreman 1980). Brothers (1980), in a recent review of age and growth studies of tropical fishes, discusses the difficulties of conducting otolith microstructure research and cautions against the overzealous application of the method. Nevertheless, he also emphasizes the great potential for analyzing growth patterns by this means.

One problem to date is that all published studies have been limited to counting the total number of increments found in fish of known size and, frequently, known age. Consequently, studies have been limited primarily to larvae, juveniles, or fast-growing, short-lived species. Age determinations from large, old fish using daily growth increments are currently unavailable, presumably because otolith microstructure becomes more complicated with growth and suitable preparations become more difficult to achieve (Brothers 1980). Furthermore, some investigators have concluded that the explicit one-to-one correspondence between increments and days breaks down among older fish due to interruptions in growth (Pannella 1971, Wild and Foreman 1980).

This paper briefly reports our attempt to age large adult specimens of *Pristipomoides filamentosus* using daily growth increments of otoliths. This is a deepwater, commercial species of snapper (Lutjanidae), found in the Hawaiian Islands and elsewhere in the Pacific. A methodology is developed which estimates the total number of increments in the otolith of a fish in lieu of counting all rings. Additionally, an error estimation technique is applied to the data to assess the reliability of the determinations.

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METHODOLOGY

Specimens of *P. filamentosus* were obtained at various localities around the Hawaiian Islands by hook-and-line fishing. These were kept on ice until returned to the laboratory where both standard length (SL) and fork length (FL) were measured to the nearest millimeter. Fish ranged in size from 18 to 70 cm FL, spanning the full adult size range of the species.

Only the largest otoliths or sagittae were examined in this study and these were removed from the cranium, cleaned, washed, and dried. Samples were then embedded in casting resin and allowed to harden completely. Cast otoliths were sectioned on a Buehler Isomet low speed jeweler's saw. Thin sections were made through the focus along a frontal plane to the most distal portion of the antirostrum (Fig. 1). Sections were then polished with levigated alumina until the surface to be examined was very smooth. Samples were subsequently etched for several minutes in a 1% solution of HC1, washed, and dried. Final preparation of the otoliths consisted of mounting them on glass slides with Euparol and cover slips and allowing about 1 week for them to clear adequately.

Samples were read with a compound microscope using transmitted light at a magnification of 400X. The distance in microns (μ) between the focus and antirostral margin was first measured with a calibrated ocular micrometer. Readings were then made at selected points along the growth axis, wherever increment microstructure was sufficiently clear and interpretable (Fig. 2). At these locations, the density of increments was determined by counting the number of visible increments and measuring the axial length of the segment in which the increments were found. In addition, the axial distance between the midpoint of the sample region and the focus was measured with the ocular micrometer. As many readings as possible were made from each preparation, subject to the restriction that counts only be made in regions where increments were clear and unambiguous.

Data were summarized for each specimen by computing the ratio of segment length in microns to the included number of increments at each specific segment examined in the preparation. This figure measures the average increment width at a given point in the otolith. Plots of average increment width against distance to the otolith focus show an inverse relationship due to declining growth rate with size. Under the assumption that one increment is equal to 1 day it is possible to approximate the growth rate on a size specific basis as follows:

$$\frac{\Delta \ell}{\Delta \text{ increments}} = \frac{\Delta \ell}{\Delta t} \simeq \frac{d\ell}{dt} \qquad (1)$$

where $\Delta \ell$ is segment length in microns and Δt is time in days. This approximation is reasonable because the localized regions in which the ratios were computed rarely exceeded 2% of the total otolith length. That is to say, the finite approximation to the differential was computed on a sufficiently small scale of time and length.

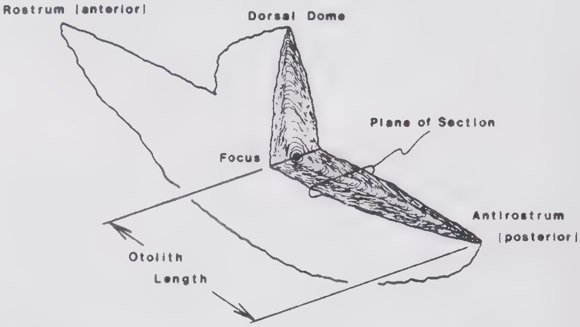

Figure 1. Schematic representation of a sagittal otolith locating the specific points of reference referred to in the text.

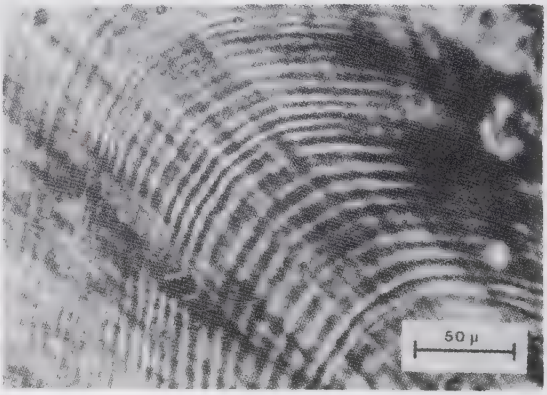

Figure 2. Slide preparation of a sagitta from *P. filamentosus* showing increment microstructure.

While plots of $\frac{d\ell}{dt}$ against length show the expected inverse relationship, there is curvilinearity apparent in the data for *P. filamentosus.* A logarithmic transformation of the growth rates removed this trend and the data were analyzed with standard linear regression techniques. The model fitted was:

$$\ell n \left(\frac{d\ell}{dt}\right) = \alpha - \beta\ell + \varepsilon \qquad (2)$$

where ℓ is length in microns, t is time in days (i.e., increments), α and β are model parameters, and ε is a normal random variable with mean zero and finite variance. Separation of variables allows solution of equation (2), which if evaluated as a definite integral, bounded by the focus and margin of the otolith, provides an estimate of the age of the sample specimen in days. More explicitly:

$$\int_{t=0}^{T} dt = \int_{\ell=0}^{L} \alpha' e^{\beta\ell}\, d\ell \qquad (3)$$

where T is the age of the fish in days at the time of death, L is the total length of the otolith at death, and α' is the reparameterized version of α from equation (2) (i.e., $\alpha' = e^{-\alpha}$). The general solution of equation (3) is:

$$T = \frac{\alpha'}{\beta}(e^{\beta L}\ 1) \qquad (4)$$

Thus estimates of α, β, and L are all that are necessary in order to estimate the age of the sample specimen.

Confidence limits for age estimations were computed using the Delta Method, a propagation of error technique (Ostle 1963, Seber 1973). Because equation (4) is a nonlinear combination of random variables (α' and β) an explicit formulation for VAR{T} is very difficult to obtain. The method used here expands the function around the mean values of the random variables in the first few terms of the Taylor Series. If terms of higher order can be neglected, then an asymptotic estimate of VAR{ T } can be obtained. The standard error of the estimate and the coefficient of variation (standard error/estimate × 100) were computed from this result.

RESULTS

As detailed in the previous section, in order to estimate the age of a specimen, one needs only the total length of the otolith (L), and estimates of the parameters α and β from the regression of otolith growth rate on otolith length (equation 2). Once ages have been estimated for a sufficient number of samples they can be related directly to the lengths of the specimens from which they were obtained, and a growth curve can be generated. This procedure bypasses potential complications due to allometric growth of the otoliths. Nevertheless, it is worth examining the relationship between otolith length and fork length to fully describe the growth process.

Figure 3 shows that, over the range of sizes examined, otolith length is allometrically related to the fork length of *P. filamentosus.* The data were fitted to the linearized form of the power function and the estimated exponent (0.631) forces the retransformed regression through the origin. This is a minor constraint because otolith formation occurs very early in life, usually during the larval stage (Brothers et al. 1976).

A total of 81 sagittae were analyzed in this study and overall these provided 2,957 separate estimates of $\frac{d\ell}{dt}$ along the antirostral growth axis. The data were pooled initially and the natural logarithm of growth rate computed. The results are plotted against distance to the otolith focus in Figure 4.

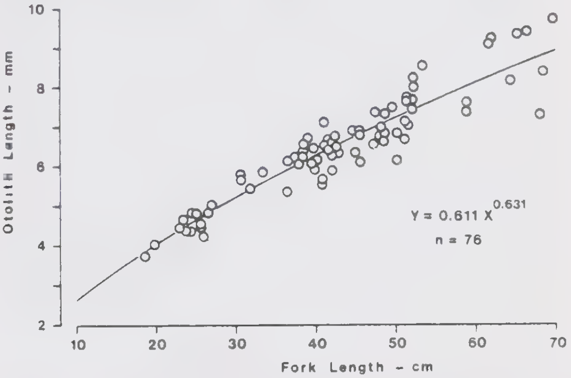

Figure 3. The relationship between otolith length (focus to most distal antirostral margin) and fork length in *P. filamentosus.*

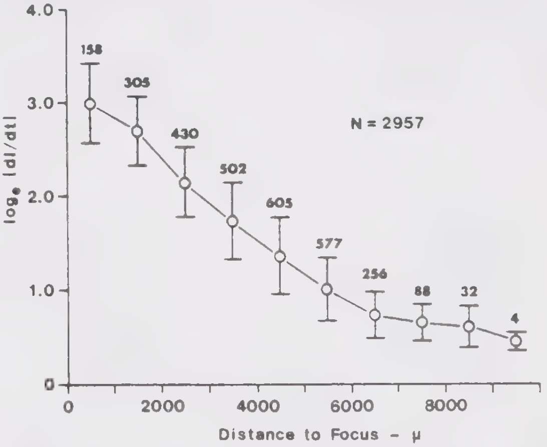

Figure 4. Pooled growth rate data for all 81 sample specimens. Circles are means bracketed by standard deviations. Numbers above are sample sizes for each length class.

It is apparent that after the otolith reaches 6,000 microns in length, an alteration occurs in the rate at which growth rate declines, maintaining a higher rate than would otherwise be expected. *Pristipomoides filamentosus* reaches reproductive maturity at about 38 cm FL (unpublished data), showing a close correspondence to this particular otolith length (see Fig. 3). These two observations are counterintuitive to one another and together they suggest that growth interruptions may commence in this species at sexual maturity. If true, an incomplete otolith time record would result, tending to lead to an overestimation of growth rates. This hypothesis may explain the higher than expected growth rates of large fish as illustrated in the figure. Consequently, all data gathered at otolith lengths in excess of 6,0000 microns were treated as equivocal and excluded from all remaining analyses. This reduced the total number of density observations from 2,957 to 2,585. Separate model regressions were then performed for each of the 81 sample specimens using the restricted date set. Age estimates were computed according to equation 4.

One means of evaluating the reliability of the age estimates obtained is to examine the frequency distribution of the coefficients of variation. Of the 81 samples analyzed, 14 had coefficients of variation greater than 10%. Figure 5 shows that the median value of this distribution is 6%. Thus, a typical preparation provides an age estimate for which the 95% confidence interval of age is ± 12% of the estimate. It follows that for individuals up to 4.2 years of age it is possible, on the average, to assign to them an age in years with 95% confidence. Estimates from older specimens become less precise. The certainty with which age can be assigned to the nearest year drops off to 75% for individuals between 7 and 8 years old.

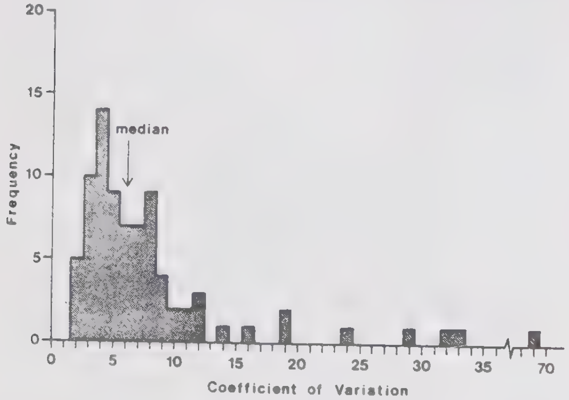

Figure 5. Frequency distribution of coefficients of variation (standard error of age estimate/age estimate × 100) from the regression model (n = 81).

The ability of the regression model presented in equation 2 to explain variation in otolith growth rate ($\ell n \frac{d\ell}{dt}$) is summarized in Figure 6. The median value of the frequency distribution of coefficients of determination (r^2) obtained in this study is about 77%. Hence, the regression approach utilized here appears reasonably effective in explaining variation in growth rate and ultimately in predicting growth patterns.

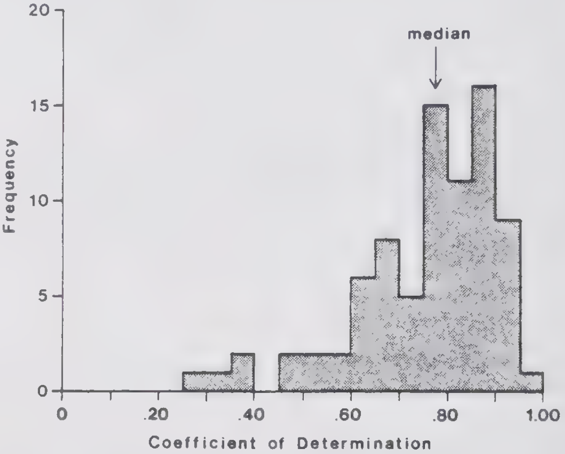

Figure 6. Frequency distribution of coefficients of determination (r^2) from the regression model (n = 81).

The results presented in Table 1 summarize the estimates of the parameters α and β , as well as the sample sizes of the 81 regressions. Variation in the two regression parameters is attributable in large part to variation in growth among individuals of *P. filamentosus* within the population. While some of the variability is due to the estimation procedure itself (approximately 19% for α and 22% for β), most is caused by natural variation in growth among individuals. The average sample size of the 81 regressions was 31.9. In other words, approximately 32 separate density estimations were used in each otolith examined after the equivocal data were deleted.

When the fork lengths of the sample specimens are plotted against their estimated ages (Fig. 7) the general pattern of growth in *P. filamentosus* emerges. Only 57 points are presented in the figure because estimations whose coefficients of variation exceeded 10% were omitted. Furthermore, several of the points are based on the average of two determinations taken from the left and right sagittae of the same fish. Thus, the points presented in this figure represent all of the fish (as opposed to otoliths) for which accurate estimations were obtained.

DISCUSSION

Several assumptions, both explicit and implicit, are made when the model (equation 3) is applied to

Table 1. Summary of regression parameter estimates and sample sizes from the increment density model.

	Mean	Standard Deviation	n
α parameter	3.16	0.465	81
β parameter	0.00040	0.00011	81
Sample size of regressions	31.9	12.9	81

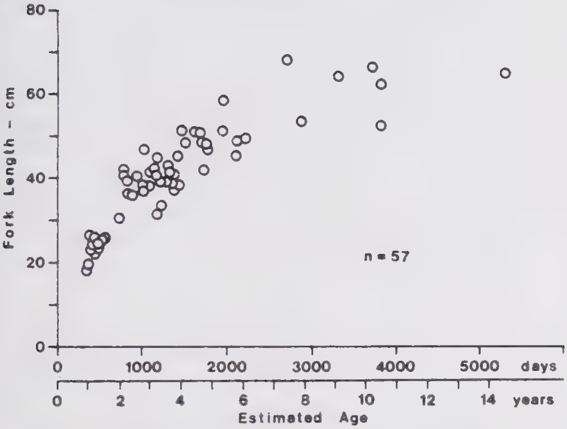

Figure 7. The relationship between estimated age and fork length in *P. filamentosus.*

increment density data taken from otoliths. One is that it is appropriate to use the interpolative power of the regression equation to predict growth rates in intermediate regions where microstructure is visually ambiguous. This assumption implies that similar processes are occurring in regions of the otolith that appear different. It is not an unreasonable assumption, however, because one can enhance the quality of a sample simply by increasing the amount of time and care devoted to a preparation, bringing out distinct increments in regions which otherwise would remain uninterpretable. Presumably, the visual quality of a preparation is largely limited by the ability of the investigator to unveil its contents.

A second and more important assumption is that it is reasonable to extrapolate the growth of reproductive individuals based on the pattern of growth preceding gonad maturation. Because all data gathered at otolith lengths in excess of 6,000 microns were deleted, age estimates obtained from the model (equation 3) are bound by this constraint. Based on the information provided by Figure 4 it is probable that otolith increments become useless as chronometers past maturity due to the existence of growth interruptions. Both Pannella (1971) and Wild and Foreman (1980) reached similar conclusions in their studies of *Urophycis chuss* and *Katsuwonus pelamis,* respectively. Clearly, if the additional energy burden incurred at maturity is substantial, extrapolation beyond 6,000 microns may be an unrealistic assumption and the growth rates of large fish may be overestimated. In this regard, it is worth noting, however, that the proportion of ovarian tissue to total body weight in *P. filamentosus* is not great, ranging from 1 to 4% among Stage III spawning females (unpublished data). Similarly, most of the accepted models of fish growth (von Bertalanffy, Gompertz, etc.) do not treat maturity as a growth singularity, i.e., a time at which the pattern of growth changes abruptly. Nevertheless, this is a critical assumption and future research in this area is planned.

A final assumption is that one increment takes 1 day to form. Other evidence, to be reported on elsewhere, has been gathered which strongly supports the conclusion that increment periodicity is daily in *P. filamentosus,* at least for individuals less than 40 cm FL (see above). Marking of otoliths in vivo by tetracycline injection, shifts in field sampled size-frequency distributions, and comparisons with the growth rates of other snapper species using an "auximetric grid" (Pauly 1980), all indicate that this assumption is realistic.

Given the above assumptions, the model appears to be effective in describing patterns of growth. The frequency distribution of coefficients of determination (Fig. 5) shows that a large percentage of the variation in growth rate within individuals (77%) is accounted for by this simple approach. Furthermore, estimates of age appear sufficiently precise (coefficient of variation $\simeq$ 6%) to assign ages to relatively old individuals. It is important to note that in the expansion of equation 4 about the expected values of the parameters α and β, the higher order terms, do tend to zero as sample size increases. Thus, in this case, the Delta Method does provide a formulation for the asymptotic variance of the age estimates.

The actual model of growth fitted to the data (equation 2) deviates somewhat from the standard von Bertalanffy growth curve (Fabens 1965, Ricker 1975). The latter model assumes $\frac{d\ell}{dt}$ to be a decreasing, linear function of length, rather than $\ln\frac{d\ell}{dt}$ as presented here. The outcome of the present method of curve fitting is to postulate that no upper bound on size exists. Given an infinite amount of time to grow, based on the empirical evidence, *P. filamentosus* should approach infinite length and not an asymptotic L_∞. Other authors have reached similar conclusions with other species of fish (see for example Parker and Larkin 1959, Paloheimo and Dickie 1965).

Acquisition of age and growth data for tropical species of fish is of great practical importance. Pauly (1980) has shown that it is possible to estimate the rate of natural mortality given estimates of the basic growth parameters. In addition, an age-length key can be generated using the results presented in Figure 7 (manuscript in prep.). Once mortality rates have been calculated it is possible to undertake an analysis of growth overfishing (Beverton and Holt 1957) and rational decisions concerning the management of exploited stocks of tropical fishes can be made. At present this type of approach is uncommonly applied to tropical stocks due to the difficulty in attaining age and growth estimates.

Many tropical species have never been aged because of uniform growth and related difficulties. The method presented here may help overcome some of these problems, if the previously discussed assumptions can be satisfied. Most important is to verify the periodicity of the increments the investigator is studying and to assess the likelihood of growth interruptions. While this field of research is becoming reasonably well established, it is premature for researchers to rely on the literature to validate their own interpretations. Much more experimental work is needed first.

ACKNOWLEDGEMENTS

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Fisheries on Coastal Pelagic Schooling Fish

Paul E. Smith

Fisheries on Coastal Pelagic Schooling Fish

Fishery science is undergoing a transition from the management of "stocks" of fish to the management of the entire fish component of an "ecosystem." The major barriers in this transition in the pelagic biosphere are not the construction of theoretical models but are likely to be the logistical problems of assembling verification of theory from field observations.

The nature of the transition from fish stock management to management of the fishery elements in an ecosystem is in part apparent from the broadly-based studies of the California Cooperative Oceanic Fisheries Investigations (CalCOFI). Following the 1947 collapse of the northern "stock" of the Pacific sardine, then the largest fishery of the United States, the CalCOFI program was instigated and funded by the fishermen and organized by Dr. Frances Clark, director of marine research for the California Dept. of Fish and Game, Dr. O. Elton Sette of the U.S. Bureau of Commercial Fisheries, and Prof. Harold U. Sverdrup, director of the University of California Scripps Institution of Oceanography. Their broad mandate was to determine the causes of the major fluctuations of production of fish stocks in the California current region.

From the CalCOFI research program it is apparent that multispecies fishery management in the context of an ecosystem will require several intermediate steps from our current skills at stock management. To emphasize the massive scope of such a transition, the survival of a year-class of fish like anchovy or sardine off California may depend on food strata less than a meter thick; at the same time these fish may be preyed upon appreciably (Smith, 1978a) by young albacore spawned 10,000 kilometers away in the western tropical Pacific or by northern fur seal females born 10,000 kilometers away in the Bering Sea.

Definitions

(1) Stock—that portion of a fish subpopulation available to a fishery. This could be the entire subpopulation.

(2) Subpopulation—that portion of a population which is likely to be interbreeding.

(3) Population—that portion of a species which is alive at a particular time.

(4) Species—a group of organisms continuous in time which was likely to be capable of interbreeding.

(5) Guild—a group of populations dependent on the same set of populations for food.

(6) Ecological community—a group of populations likely to be found together.

(7) Ecosystem—a community of organisms and their environment.

The most critical stage of the transition from stock management to ecosystem management from a fisheries standpoint is the guild. In the California Current system and several other productive areas of temperate and tropical seas, the guild of schooling pelagic organisms is an obvious repetitive feature. The major populations of schooling pelagic organisms in the California Current are the northern anchovy, *Engraulis mordax;* the Pacific sardine (or pilchard), *Sardinops sagax;* the jack (or horse) mackerel, *Trachurus symmetricus;* the Pacific mackerel, *Scomber japonicus;* the Pacific saury, *Cololabis saira;* the Pacific hake (or whiting), *Merluccius productus;* and the market squid, *Loligo opalescens.* The guild depends to varying degrees on large phytoplankton, zooplankton, and small fish. Most of the same genera occur together off Europe, South Africa, Australia, Japan, and the west and east coasts of South America, and major fisheries concentrate on the schooling pelagic guild. As repetitive as the group of genera is the tendency for the major stocks to collapse under fishery pressure.

The importance of the guild of coastal pelagic schooling organisms is that it is a human protein source perpetually capable of providing several kilograms of fish per year per capita of the world population. These fish are close to land, and their tendency to be schooled and for the schools to be aggregated makes their capture very efficient by concentrated purse seine fleets. This capture efficiency is also a major hazard to the perpetuity of the yield, and recurrent collapses of members of the pelagic schooling guild are the topics of much applied research in each region of the world where these fisheries occur. The inevitable fluctuations in the available stocks may be smoothed at the market place because canned and fish meal products can be stored for extended periods.

Schooling pelagic fish occupy a hydrographic province whose geopraphic extent can double or triple in a few years and return to the original as rapidly. Also, a pelagic schooling fish occupies a very small portion of its available environment at any instant, but it occupies it very intensely. For instance, we have data which suggest that under each square meter of sea surface there may be 15 kilograms of fish within a fish school (Hewitt et al., 1976). The fish schools occupy only 0.5 percent of the area which is physiologically defined for them. The early nomenclature, particularly density-dependent and density-independent, is generally inadequate for describing survival in schooling fish. Where the habitat is geographically circumscribed, stock size dependence and density dependence may be identical, but in an area of flexible hydrographic boundaries, density dependence operates on a local scale, such as on the kilometer scale, and stock size dependence operates on a scale of hundreds of kilometers. This distinction is very important for monitoring a fishery because the fishery normally operates not over the ecological range or the entire hydrographic province on which the fish depend, but only over a small part of the habitat where fish concentrate from time to time and are likely to be encountered by fishing boats.

The Pacific Sardine

What really did happen to the Pacific sardine? Our perception of the situation is necessarily simple, because we lack data necessary to erect a complex hypothesis. However, our perception of what happened to the Pacific sardine was important for determining the research attack taken at the Southwest Fisheries Center and for explaining why we are spending so much time in the area of larval and juvenile studies.

The Pacific sardine once occupied an area from the tropics to Vancouver Island. The virgin population was made up of about ten spawning year classes in addition to the year classes about to recruit, and the older ones of these migrated along the entire west coast of America. There were three stocks. One stock we call the northern subpopulation of the Pacific sardine and it is this one that spawned in the spring, roughly from the upwelling area off Punta Eugenia, Baja California, to San Francisco. Another subpopulation occurred south of Punta Eugenia, and one still occurs in the Gulf of California. The limit to spawning was the 13°C isotherm; Pacific sardine eggs do not survive in water colder than 13°C. Following spawning, it appears that the older fish migrated to the north, somewhat in proportion to their size—the largest fish traveling the furthest—and separated out along the coast to feed in the extremely rich area which terminates the west wind drift of the Northern Pacific Ocean. It is, as well, the primary site of an eastern boundary current upwelling system. There they gained weight for the season and moved back to southern California the following spring to spawn.

The time course of the Pacific sardine fisheries has been assembled by Ahlstrom and Radovich (1970). The Pacific Northwest landed up to 100,000 tons and became the first area to notice the changing migration patterns of the Pacific sardine. The fishery there virtually stopped in 1945 and has not yet recovered. Central California was the primary site for phytoplankton production and the place of the largest fishery, half a million tons. The sardine fishery there had collapsed by the end of 1955, after two population failures. Southern California, the residence of the younger sardines, had a sustained fishery that lasted into the 1960s and then it too was abruptly terminated in

1964. The Baja California fishery caught both the southern and northern stocks; it now catches anchovy while it continues at a low level of sardine fishing. That fleet shifts seasonally into the Gulf of California, where the primary sardine fishery is now conducted.

Murphy (1966) described what happened to the Pacific sardine. The Pacific sardine had ten spawning year classes in the virgin stock. Since short-term anomalies in the environmental conditions are more common than long-term anomalies, the sardine, which has ten spawning year classes, is not very prone to periodic recruitment failures. However, when the sardine population was reduced to a population having only two spawning year classes: two recruitment failures in a row virtually destroyed the stock. Murphy believes that this is the direct effect of fishing because fishing changes the age composition of the stock. This final age composition was then more vulnerable to shorter and shorter term environment anomalies, which eventually destroyed the stock.

I have made a slight addition to the Murphy hypothesis regarding reducing the number of year classes to two. I believe it is also true that anomalies which cover small areas are more common than environmental anomalies which cause year-class failure over a large area. The sardine stock collapsed from north to south. This probably also implies that the sardine occupied a smaller and smaller area of the pelagic environment and, having occupied these smaller areas, was then more subject to anomalies over a small area. The changing year-class structure is the basis of Murphy's main hypothesis on why the Pacific sardine collapsed. Added to this is the probability that a smaller distribution area is more subject to destructive anomalies.

The Sardine Investigation and CalCOFI

CalCOFI is the California Cooperative Oceanic Fisheries Investigations. It was begun by state, federal, and university scientists at the request of the fishermen and processors who were put out of business by the drastic sardine population collapse. The industry wanted to know if population variations could be predicted and if fishery regulations would shield it from these variations.

To find out, they taxed themselves from 1947 to 1978 a dollar a ton on all of the "wetfish" catch to support research on pelagic California commercial fish. The fishermen themselves were interested enough to find the causes for these drastic declines in population. They took a large fraction of their catch dollar and put it toward specific research to study these variations. Even though the actual dollar amount was never very large in terms of a major fishery research program, the program guided and coordinated the research of three major organizations for more than thirty years. So the less than half a million dollars put in by the fishermen out of their own pockets guided the use of four or five times that much research money over this period.

The primary reason the processors and fishermen withdrew their financial support in 1979 was not that they were unhappy with the progress, but that the federal Fishery Conservation Management Act (FCMA) 200-mile-limit legislation had taken the responsibility for the management of these fish, and it was concluded at this time that private industry could now retire from its funding of these activities. Today the primary research components of CalCOFI—the Southwest Fisheries Center of the National Marine Fisheries Service, the California Department of Fish and Game, and the Marine Life Research program of the Scripps Institution of Oceanography—continue their research in the same coordinated fashion but with broader objectives.

Field Studies

The primary activity of CalCOFI has been the field population study. A large proportion of ship time was planned around studying pelagic schooling populations in the field. This was not done at the expense of monitoring the catch in the age, weight, condition, sex ratio—those programs continued. Two additional surveys were mounted. One was a sea survey of juveniles and adults conducted by the California Dept. of Fish and Game. They began by attracting fish to night lights and catching them with lift nets or dynamite. Their techniques for studying sardines had to be modified so that they could also study anchovy, jack mackerel, and Pacific mackerel.

The second major field population survey was conducted on eggs and larvae. In 1949, when high seas oceanographic work started, there was no capability to capture adults on a routine basis over their entire range. One solution was to monitor spawning behavior, stock size, and spawning. Particularly important to the interpretation of field data has been the laboratory study phase which began in the mid-50s.

What do we expect from a larval survey? At the beginning, larval surveys to determine distribution and abundance of eggs and early larvae were supposed to give us an index of the spawning biomass; the later larvae were to be used to project how many survivors there would be from each year's spawn. The precision of larval surveys is greater with small stock sizes than it is with large stock sizes. The catch-per-unit-of-effort monitoring, done when a fishery is operating, is accurate with a large stock size and becomes less dependable with small stocks. The larval survey therefore augments the normal fishery monitoring in a useful way. The spawning surveys also monitor changes in spawning biomass. One obvious shortcoming has been that the best estimates of the abundance of surviving large larvae will not predict in a correlative sense the size of the recruitment.

Ahlstrom (1965) examined the CalCOFI larval surveys, the recruitment of fish into the fishery, and the oceanographic conditions on the spawning grounds. He reasoned that variations in "general productivity" could not have

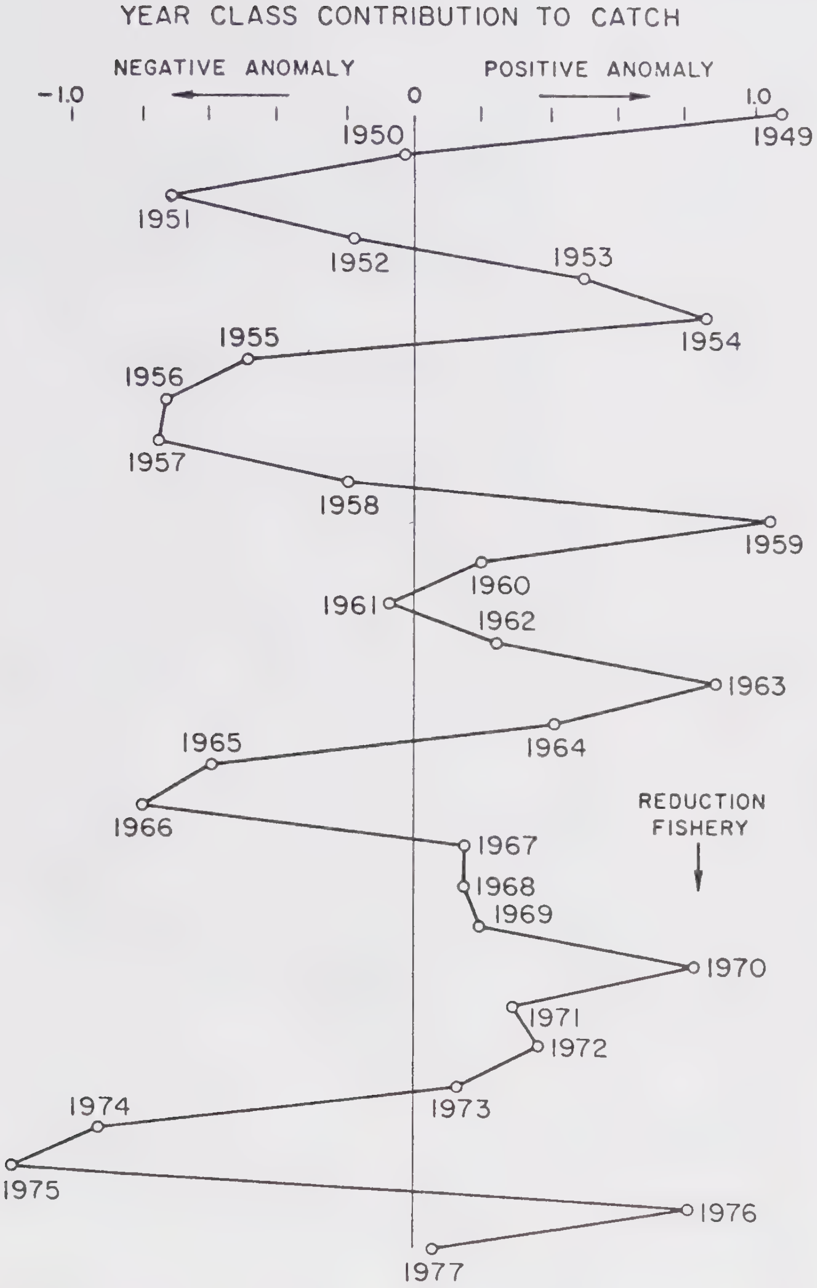

Figure 1. The central population of northern anchovy year-class contribution to catch. The numerical contribution on each year's catch by each year-class is calculated from the sum of the proportionate contribution for the first through fourth years. The sum was normalized for the purpose of constructing a bilaterally symmetric time series with a mean of zero, and the anomalies are expressed in the number of standard deviations. The fisheries before 1966, from which these data were derived, were small and local. The reduction fishery, which began in 1966, has been sampled by the California Dept. of Fish and Game in the Los Angeles area (after Smith et al., in press).

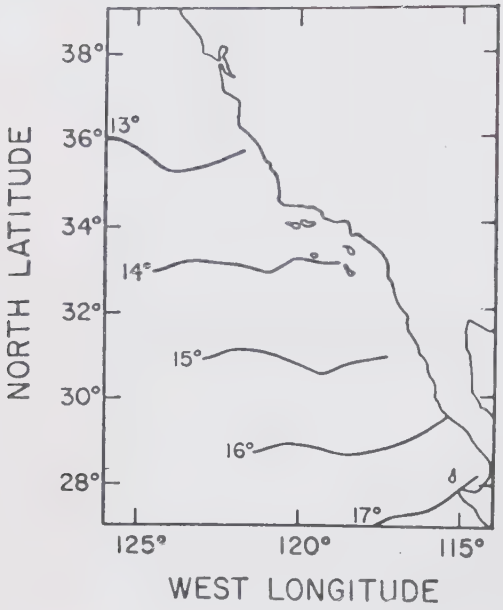

Figure 2. The arithmetic mean temperature at 30 meters depth for January from 1950 to 1968 is derived from a regional summary of CalCOFI standard depths. The 14°C isotherm is oriented zonally at 33°N latitude.

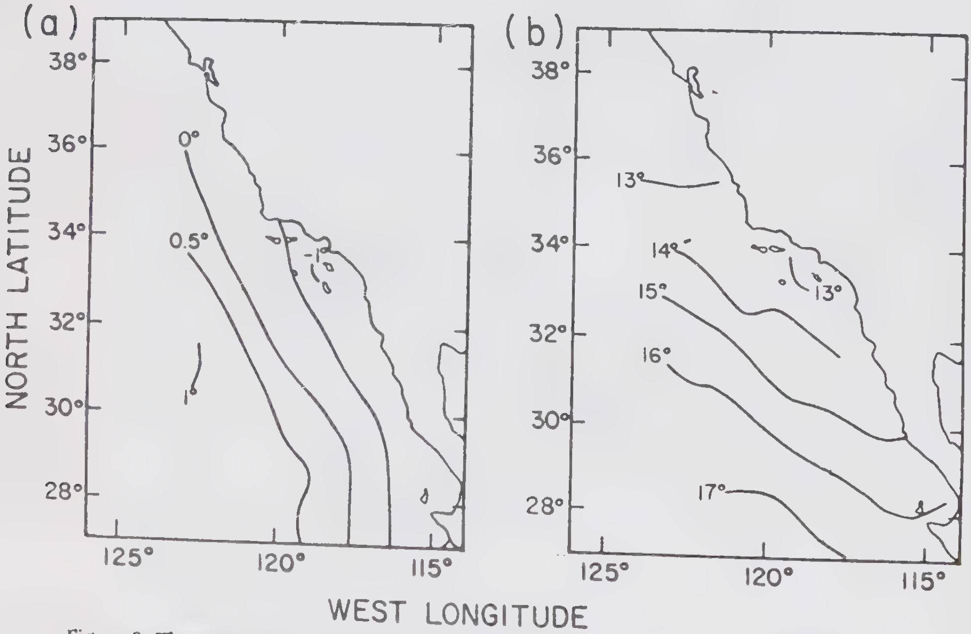

Figure 3. The 30-meter temperature anomaly (a) and temperature (b) at the first of four negative anomalies in the contribution to catch (Fig. 1), January 1951. The 14°C isotherm is oriented diagonally and the 13°C isotherm is in the Southern California Bight. The anomalies are oriented meridionally; and regional anomalies are negative within 100 n.mi. of the coast: part of the Southern California Bight has more than 1°C negative anomaly.

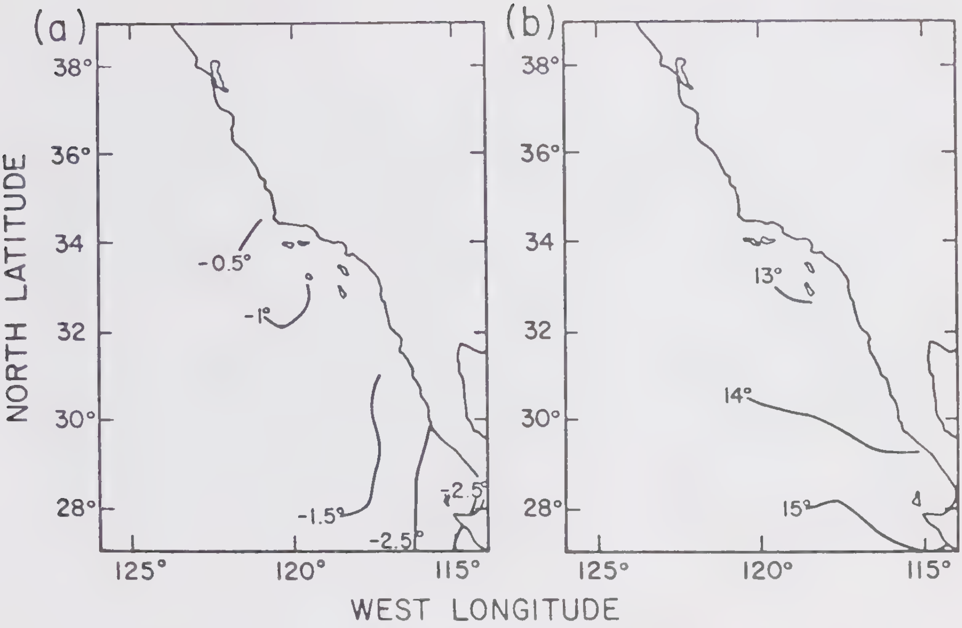

Figure 4. The 30-meter temperature anomaly (a) and temperature (b) at the second of four negative anomalies in the contribution to catch (Fig. 1), January 1956. The 14°C isotherm is at 30°N latitude, 180 miles south of the mean position. The 13°C isotherm encompasses the Southern California Bight, and the anomalies of from 0.5°C to 2°C colder than normal over the entire distribution of the central subpopulation of the northern anchovy.

been a major control on these fish stocks because a general decline should have been observable in all species, but the good years for anchovy, sardine, and Pacific mackerel did not coincide. In fact, he stated, some of the "poorest years for larval survival have been years of high productivity," as measured by high standing crops of sardines. Even with these changes in the success of year classes, he found no significant variation in relative numbers of large larvae and concluded "this consistency pulls the rug out from under any attempts to relate variation in larval survival to environmental conditions." At the time of his study, only eight annual surveys (1951–58) had been analyzed.

Twenty-nine years of age composition data have been assembled from the bait, cannery, and reduction fisheries on the central subpopulation of the northern anchovy (Fig. 1). Large-scale features of the California Current were examined for some of the maxima and minima in anchovy year-class "contribution to catch," a measure of spawning success (Smith and Haight, 1980). One constant feature, a large-scale cold anomaly in the Southern California Bight (Smith et al., in press), coincided with the four episodes (1951, 1955–56–57, 1965–66, and 1974–75) of anomalously low contribution to catch. Moderate and high contribution to catch resulted indiscriminantly from average and warm conditions.

The diagnostic sign of these years of poor contribution of a year-class to catch may be seen from comparing the average January temperature at 30 meters over the distribution of the northern anchovy central subpopulation (Fig. 2) with the same temperatures in January of 1951, 1956, and 1975 (Figs. 3, 4, and 5) and their resultant anomalies. The average plot has the 14°C isotherm parallel to and overlying 33°N latitude. In the "cold" years the 14°C isotherm is no longer parallel to or overlying 33°N latitude. The nearshore end is replaced by 13°C water. An estimate of abundance of the larger larvae (15 mm) similarly shows some concordance with the "poor" recruitment years (Fig. 6).

Not only the abundance but the timing of the peak abundance of large larvae appears important. In the failing years—1951, 1956, 1965, 1966, and 1975—the spring and summer abundances were low. None of the regional average temperatures shown is near the lethal limit for anchovy (Ahlstrom, 1965), so one must conclude that the temperature is an indicator rather than the cause of adverse conditions for survival. Some of the possible causative factors (such as low vertical stability and mixing) will be discussed in the following section.

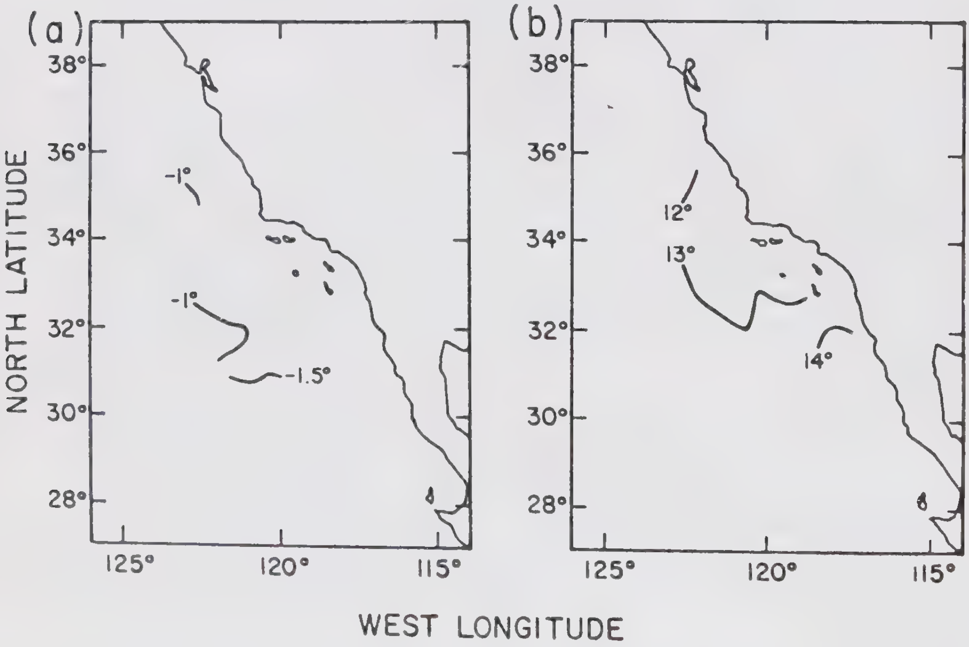

Figure 5. The 30-meter temperature anomaly (a) and temperature (b) at the fourth of four negative anomalies in the contribution to catch (Fig. 1), January 1975. The 14°C isotherm has been replaced by the 13°C isotherm, and the temperature anomaly is from 1°C to 1.5°C below average over the whole distribution of the northern anchovy.

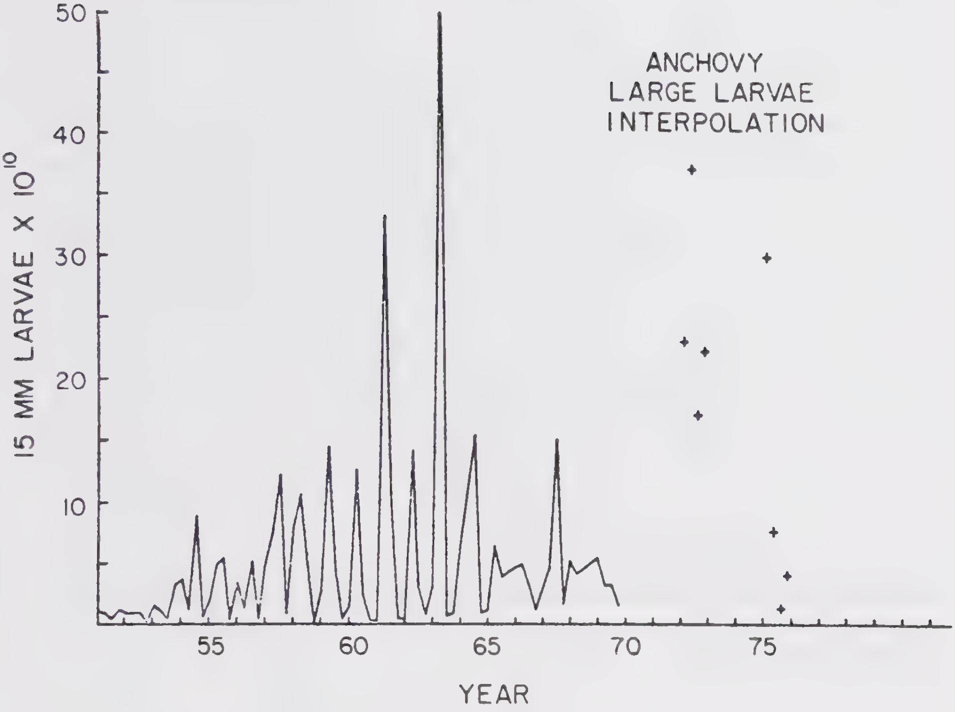

Figure 6. Estimated abundance of 15 mm standard length anchovy larvae, 1951 to 1975. Low relative contribution to catch occurred in four sets—1951, 1955–56, 1965–66, and 1974–75. Moderate and high contribution to catch cannot be distinguished at the 15 mm stage. Values are quarterly estimates which result from single cruises in 1961–65; in other years the quarterly values result from more than one cruise in winter, spring, and summer and usually a single cruise in autumn.

Sampling to Determine Anchovy Larval Mortality in the Sea

It is impossible to make unbiased estimates of the number of fish larvae in the sea, and precise estimates require many carefully taken and sorted samples. The major biases are caused by extrusion through the meshes of nets used to capture embryos and early larvae and evasion of the approaching net by older larvae. The major source of imprecision is the tendency of larvae of all sizes to be aggregated, or "patchy." Larval mortality may be determined from a sufficiently large set of imprecise samples by monitoring the sources of bias. We may begin to specify small-scale sampling requirements for describing larval mortality by examining the mass effects of mortality on a very large set of samples (> 30,000) over the CalCOFI grid area (200,000 sq.n.mi.) for the 24-year period, 1951–1975.

It would be foolhardy to specify sampling requirements in detail without some information on a hypothesis to be tested. For example, a space-extensive survey might be required to test the null hypothesis about larval transport—"no important effects on mortality are due to the area in which they are spawned." A time-intensive survey would be required to test the null hypothesis about critical period—"no discernible differences in mortality occur over short periods." Thus for a widely distributed species like the northern anchovy, a test of the "larval transport" hypothesis would require a different sampling emphasis from a test of the "critical period" hypothesis.

For the purpose of this chapter, then, I will discuss some significant sources of bias and how a sampling program would be established to test several hypotheses relating to larval anchovy survival in the sea. Knowledge of the distribution of mortality in the life cycle, variations in mortality, and models of cause and effect should provide background for rational management of a fishery on this stock by direct monitoring and prediction of recruitment and population size.

Anchovy mortality is extremely high, and each successive life stage represents an improving chance for survival (the "Type IV" survival curve of Slobodkin, 1962). I have arbitrarily divided the life cycle into six stages: embryonic, early larval, late larval, juvenile, prerecruit, and adult. In Table 1, I have listed these stages with nominal durations, estimated daily mortality rates, and the abundance of a hypothetical cohort spawned in a week and evaluated at each of the stage margins. The model has been constructed so that crude estimates of fecundity (Hunter and Goldberg, 1980) allow the population model to represent a stationary population (Fig. 7). The model is

Table 1. Example of negative binomial weighted model solution for 14 size groups of anchovy larvae (Bissell, 1972; Zweifel and Smith, 1980).

Group	Preserved size (mm)	Recorded preserved size (mm)	Average* live size (mm)	Age from spawn (days)	Days in interval	Predicted LCL	Predicted UCL (No. 10m^{-2})	Predicted Mean
1	3.25	2.5	3.23	1.98	1.95	3.1×10^2	4.8×10^2	3.9×10^2
2	3.25–4.25	3.75	4.49	6.45	4.69	1.8×10^2	2.5×10^2	2.1×10^2
3	4.25–5.25	4.75	5.57	9.32	2.67	1.1×10^2	1.5×10^2	1.3×10^2
4	5.25–6.25	5.75	6.62	11.84	2.40	6.8×10^1	9.0×10^1	7.8×10^1
5	6.25–7.25	6.75	7.66	14.14	2.21	4.2×10^1	5.5×10^1	4.8×10^1
6	7.25–8.25	7.75	8.68	16.27	2.07	2.6×10^1	3.4×10^1	3.0×10^1
7	8.25–9.25	8.75	9.68	18.29	1.97	1.6×10^1	2.1×10^1	1.8×10^1
8	9.25–10.25	9.75	10.69	20.22	1.90	1.0×10^1	1.3×10^1	1.2×10^1
9	10.25–11.25	10.75	11.69	22.09	1.85	6.2×10^0	8.3×10^1	7.2×10^0
10	11.25–12.25	11.75	12.68	23.92	1.81	3.8×10^0	5.3×10^1	4.5×10^0
11	12.25–13.25	12.75	13.68	25.71	1.78	2.3×10^0	3.4×10^1	2.8×10^0
12	13.25–14.25	13.75	14.68	27.48	1.76	1.4×10^0	2.2×10^1	1.8×10^0
13	14.25–15.25	14.75	15.67	29.24	1.76	6.7×10^{-1}	1.1×10^1	8.6×10^{-1}
14	15.25–16.25	15.75	16.66	30.97	1.71	5.2×10^{-1}	9.0×10^1	6.9×10^{-1}

* Corrected for abrasion and shrinkage (Theilacker, 1980).

LCL = lower confidence limit.

UCL = upper confidence limit.

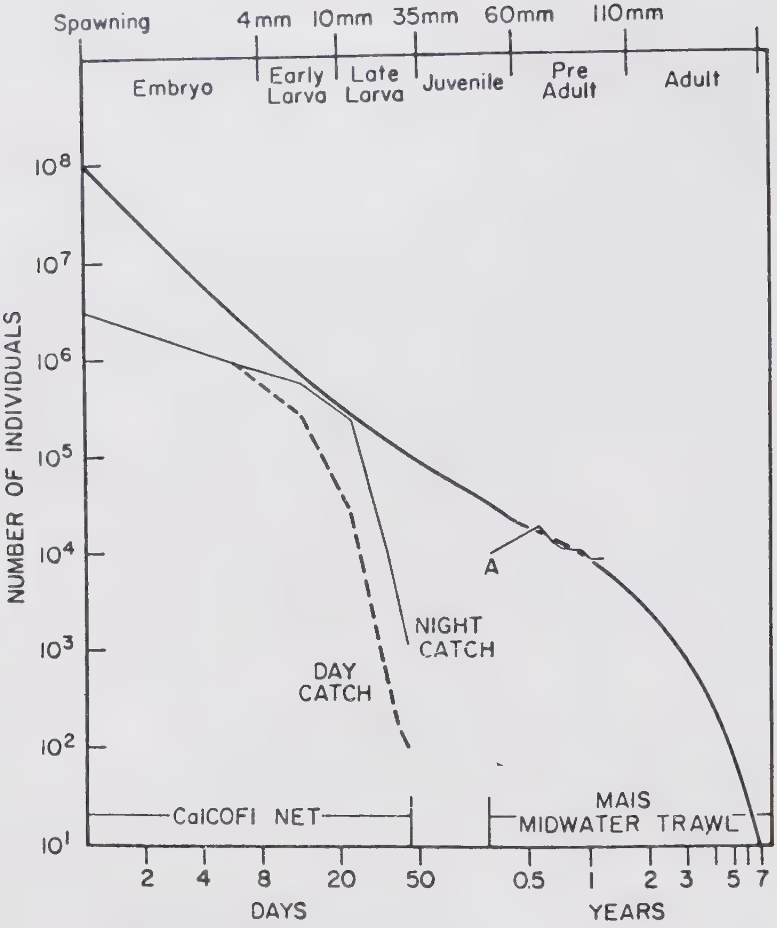

Figure 7. A comparison of a total life history model of the northern anchovy central subpopulation and sample data from the CalCOFI standard silk net (Kramer et al., 1972) and the California Dept. of Fish and Game midwater trawl (Mais, 1974). The main bias at the embyro stage is extrusion through the mesh of the net. The main bias of the early larval stage is daytime evasion of the net, and the main bias of the late larval stage is day and night evasion of the net. Further evidence of nighttime evasion of nets by fish larvae contained in a plankton purse seine compared with a towed plankton net is given by Murphy and Clutter (1972). The point "A" represents occasional juvenile anchovy captured in the midwater trawl liner. These juveniles may be underestimated by behavioral, geographic, and bathymetric differences from the adults.

artificial because absolute mortality rate estimates are available only for the early larvae (Zweifel and Smith, in press) and for the adults (MacCall, 1974). These rates are joined only to satisfy the condition of stationarity. The reader is cautioned that the population of anchovy probably does not exhibit stationarity and that all estimated rates have been assembled from multiyear samples over wide ocean areas.

Biases

Four biases have been evaluated: escapement, extrusion from nets, evasion from nets, and stage duration. The first three are negative biases, but deviation in stage duration can contribute either a positive or a negative bias. The nature of these biases is discussed here in preparation for the next section on sampling procedures and program (tactics and strategy) for the analysis of population change through studies of mortality at sea. Another bias may result from statistical transformation of abundance data.

Escapement

Escapement is defined here as the passage of the sampled organism through the mesh apertures of a net. A major consideration, then, is the size of the mesh aperture. As a first approximation it may be assumed that escapement will occur when the minimum dimension of the anchovy larva is less than the diagonal of the mesh aperture. The selection of an appropriate mesh aperture is important because larger apertures yield variable retention when, for example, filamentous algae impart retention characteristics of smaller nominal mesh apertures. Smaller than necessary net apertures retain more plankton from which the larvae will have to be sorted; costs of sorting anchovy larvae from other plankton are high, so this too is an important consideration.

Extrusion

Extrusion in this context is the forcing of the larvae through the meshes of the net. This can result either from improper design of the net or from towing the net at too high a speed. Towing speed may be acceptable on the average, but an increase in speed near the end of the tow can extrude larvae retained for most of the tow duration. Extrusion may also be increasingly probable with the lengthening of towing time or with vertical towing in rough seas. As a first approximation, extrusion and escapement should be evaluated at tow speeds of 70 cm/sec with increments of 20 cm/sec (Smith and Richardson, 1977, Table 3.2.3).

Evasion

Evasion is the swimming of larvae out of the volume to be filtered by the net. Evasion is demonstrable from day/night (Fig. 8) differences in catch of anchovy larvae and sardine larvae as small as 5 mm preserved length. The existence of a day/night difference also demonstrates night avoidance (Smith and Richardson, 1978). For a first approximation the evasion bias can be regarded as total when the length of the anchovy larva is 3 percent of the radius of the net when the net is being towed at 5 larval body lengths per second. For bridle-free nets (which are recommended), larvae will be sampled somewhat better. Evasion will likely be reduced by improved filtration efficiency and nets with low visual contrast.

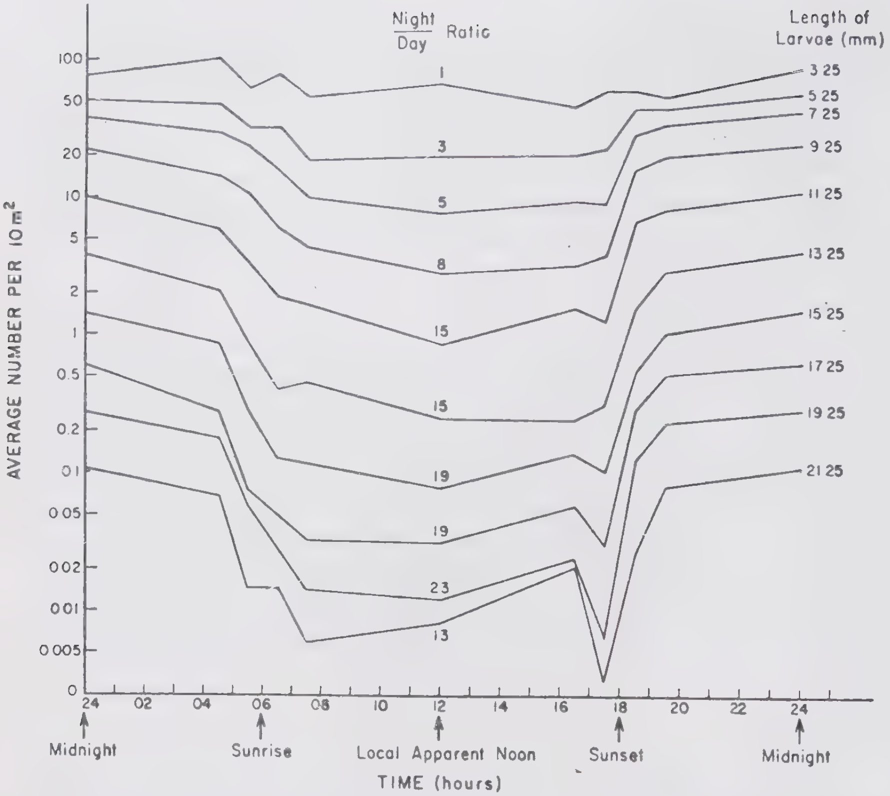

Figure 8. Larval anchovy capture by time of day and size, total California Current Area, 1951–1969. Marked asymmetry at dusk may be attributed to the tendency of larvae 10 mm standard length to approach the surface to ingest a bubble to fill the gas bladder (Hunter and Sanchez, 1977). The night to day ratio of catches is likely due to enhanced ability to react effectively to the slow approach (70 cm/sec) of the CalCOFI net in daytime.

Stage Duration

The duration of fixed arbitrary developmental stages of fish larvae controls the estimation of mortality. If all adjacent stages of fish larvae are of identical duration, a precise and accurate estimate of mortality rate is possible from relative estimates of abundance of the adjacent stages. For example, if one stage is twice as long as the following stage, the interstage mortality rate will be overestimated owing to the relative overestimate of the first stage. Of course, mortality "inversions" can occur when the second stage is so long as to appear more abundant than the first. Unbiased mortality rate estimates may be possible if stage duration is known.

1. Temperature

Temperature can influence mortality estimates over time or area by delaying larval development in colder time periods or areas leading to a longer duration at a stage and an overestimate of relative abundance. Temperature and natural variation may be the exclusive controls on development rate and stage duration in the embryonic period (before feeding) of the larvae. In anchovy the embryonic development period may be doubled by a change from 18°C to 13°C, leading to a twofold overestimate of abundance at that stage.

2. Food

Following total utilization of the yolk, the rate of feeding and energy expended searching for food may markedly influence the duration of predefined stages. No studies of the effect of feeding on duration of predefined stages have been completed. It may be assumed that variability by a factor of 2 in duration may occur in the early larval stages, and a factor of 7 seems possible for the later larvae. However, this high level of variability does not appear to be supported by the age distributions of larvae caught at sea (Methot and Kramer, 1979).

Statistical Tranformation

It seems possible to confuse the graphic (Bagenal, 1955; Aitchison and Brown, 1966) and analytical properties of the exponential decline in abundance with the statistical properties of log transformation. It is, of course, permissible as a first approximation to plot the logs of abundance versus time to obtain a linear form of the exponential mortality and to interpolate on this basis. A problem arises if, instead of plotting the log values of the stage sample means, one plots the means of the logs of the sample values. This is the geometric mean, and the use of adjacent values of the stage geometric means will lead to a bias in the estimate of mortality slope. This bias originates from either or both of two sources related to the dispersal or aggregation of the larvae—changing sample variance and changing sample coverage.

1. Sample variance

The geometric sample mean is a function of the arithmetic mean and the sample variance. Thus changes in the geometric mean have imbedded in them changes in both sample mean and variance. The general trend of mortality in larvae is also accompanied by dispersal of patches in the embryonic and early larval stages and the appearance of reaggregation in the later larval stages. The effect is that the geometric mean is a large underestimate of abundance in the more patchy embryonic stage and a smaller underestimate of abundance in the more dispersed early larval stage; a mortality rate calculated from geometric means will thus be an underestimate of the population mortality rate. Such a comparison of geometric means may even result in changing the sign of the mortality rate. Less serious perhaps in the late larvae would be the tendency for the bias of the geometric mean to be greater in a late stage, and this would mathematically induce an overestimate of mortality brought on by the reaggregation of the population into patches.

2. Log transformation

Two approaches to log transformation arise in the treatment of zero samples: (1) if one adds a constant to all sample values before transformation and (2) if we analyze positive samples only. When analyzing mortality of fish larvae, addition of a constant induces a gradual decrease in the slope owing to the larger proportionate contribution to the total of the constant. Secondly, the dispersal of the embryonic stages entails expanding coverage of the habitat, possibly reducing the number of "zero" samples for a time and changing the proportionate contribution of the added constant. Analysis of only positive samples under these same conditions results in an overestimate of the mortality rate. For different species of larvae, I consider it prudent to examine these effects before proceeding with analysis of mortality. Alternately, methods not employing logarithms could be used.

3. Weighted negative binomial

The weighted negative binomial model (Bissell, 1972; Zweifel and Smith, in press) can be used to obtain unbiased sample means and maximum likelihood estimates of the upper and lower confidence limits. The advantage of this model has no biological basis but is related to the explicit treatment of "zero observations," the use of the arithmetic mean as one parameter, and the ability to accommodate all scales and intensity of contagion from Poisson distribution to log-normal.

Sampling Strategy

Limited resources for collection of larvae at sea, sorting, identifying and measuring on land, and analysis of the data lead one to consider questions of sample strategy. From examination of CalCOFI data used for biomass assessment, one may gain some insight into sampling requirements for more specific hypotheses regarding larval mortality. Some preliminary considerations of the extent of sampling and the temporal and spatial intensity of sampling may be deduced from existing survey data. The CalCOFI surveys usually covered tens to hundreds of thousands of square nautical miles, with one station for each 800–1600 square nautical miles. Surveys were at monthly or quarterly intervals, and annual estimates of species abundance were formed from 1500–2000 samples. This data set has limitations at the smaller scale for determining sampling strategy, but the scale of patches is probably from 0.2 to 1 nautical square mile (the size and movement of a spawning school) and the period of vulnerability of larvae to a plankton net is of the order of three weeks. For this purpose we will consider six hypothetical larval mortality situations: larval transport, critical period, predation (including cannibalism), starvation, preschooling distribution, and spawning condition.

Larval Transport

The null hypothesis is "changes in geographic distribution of the larvae relative to the geographic distribution of spawning have no important influence on the numbers of fish which survive to become mature." To test this, one needs an estimate of the number of survivors from the cohort of interest and a set of larval samples. This set of samples must be spatially intensive to provide an estimate of mean position at several stages of larvae in the embryonic, early, and late larvae stages. The sample set for northern anchovy would also need to be temporally and spatially extensive because of the long duration and wide area of spawning from which the survivors eventually emerge. Space-time units for anchovy could be several hundred square miles at biweekly or monthly intervals from December to July. Within each space-time unit there would be sufficient precision for a useful mortality estimate from fewer than 100 samples.

Critical Period

The null hypothesis is "larval mortality is constant for all stages of embryonic larvae and early larvae, or there is a gradual improvement in survival as the larvae differentiate sensory and locomotor structure." The term "critical period" is an aquarist's phrase for the transition from rearing yolked larva stages to those requiring the provision of the proper kind and amount of food. It is reasonable to assume that first-feeding is also important in nature. The demonstration of this phenomenon at sea should probably begin with temporally intensive sampling over a small area near the maximum concentration of larvae. Because the embryonic stages and the early larval stages which ensue are still highly aggregated following the schooled spawning, adequate precision of estimates of the mean and standard error of the mean will require 500–1000 samples taken with sufficent precaution to eliminate escapement or extrusion through the meshes at the time of hatching. Mesh size should be 0.333 mm for northern anchovy, and the total volume filtered should be kept low to minimize variance.

Predation

The null hypothesis is "species 'A,' which coincides in space and time with the anchovy eggs or larvae, does not prey on the anchovy to such an extent that the anchovy egg or larva mortality rate is appreciably changed." In the test of this hypothesis, one requires spatially intensive samples which are adequate to sample both predator and prey. For example, in the special incidence of "cannibalism" it was found necessary to deploy plankton nets with 0.333 mm mesh and in the same area to deploy commercial-scale trawls to capture the adults. Other predators could require intermediate net sizes or could be obtained from the same samples as required to determine the larval mortality rate. To assemble a model of changes in larval mortality rate as a function of changes in the coincident populations of predators, the quantitative deployment of several scales of samples is required. It does not seem likely that population models for predators will be necessary on this time scale.

Starvation

The null hypothesis is "in nature the larval mortality rate is not affected by the amount, kind, spatial distribution, and production of food organisms." To gather evidence for this hypothesis, one would need the usual spatial and temporal intensity of sampling required to define larval mortality and the ability to sample with high spatial definition the food of the anchovy larvae. This would require the coupled deployment of sampling equipment with sufficient retention capacity to retain the food of the larval anchovy. The food samples would need only to cover the spectrum of sizes below the sampler used for the larval samples. The smallest size of interest is determined by the acuity of the larval eyes, and the largest size of interest is determined by the gape of the larval mouth. Since the larval mortality rate needs to be monitored for several months, one needs population models of the prey organisms to estimate food production. Another aid in resolving the horizontal and vertical dimensions of spatial intensity would be a series of models concerning the formation and destruction of food aggregations. Also, the changes in larval growth under various conditions of starvation will be required to adjust the size-specific mortality rate and the time-specific mortality rate estimates.

Preschooling Distribution

The null hypothesis is "in nature there are no important regional or temporal changes in dispersal rate which would materially influence the rate of formation of schools by juvenile anchovy." The tests of this hypothesis would require verification of the size and number of juvenile fish schools as a function of the distribution and number of fish larvae from which the schools were formed. Like the "predation" hypothesis, this would require a wide range of sampling apparatus. The deployment would be different in that the predation test requires simultaneous samples while the "preschooling distribution" hypothesis requires a sequential arrangement of samples of various sizes. For example, plankton nets or pumps would be deployed for the larval mortality rate, 60 days later micronekton net samples of juveniles would be needed, and later still, commercial size samples of prerecruits and adults would have to be taken. Sample repetition and the resultant sample variance would be used to evaluate the intensity of aggregations. Determining the scale of aggregation would require high spatial intensity and continuity for resolution.

Spawning Condition

The null hypothesis is "within the observed range of physiological condition of spawning adults, there will be no important changes in the subsequent survival rate of larvae." This test would require samples of the adult anchovy for six months prior to the spawning season and temporally intense samples of the egg production and larval survival.

Conclusions

While many plausible hypotheses exist to explain the variation in survival rate of larvae and the rate of addition of young fish to the commercial stock, there have been few tests. The scarcity of tests of hypotheses is caused by the lack of identification of the spatial and temporal intensity needed for samples required for the tests of single hypotheses. The evaluation and comparison of two or more mechanisms is far more difficult, and multiple tests are likely to be necessary. This may be stated as a null hypothesis, "the fundamental cause of variation in the survival of anchovy from spawning to recruitment is the same from year to year."

Larval Anchovy Patchiness

In the previous section I pointed out how larval anchovies have been used to assess biomass. Underlying this technique is the recognition that the larvae occur in patches and that a knowledge of the causes of patchiness is central to applying this technique. An investigation of larval survival must take into consideration patchy distribution of larvae as well. Anchovy larval patchiness has many origins, among them schooling of spawning adults (Smith, 1978b), diurnal periodicity in spawning behavior, local sites of high larval mortality, dynamic oceanic events like convergence zones, and larval aggregation behavior. Unfortunately, it has not been possible to study these contributing causes to patchiness in sufficient detail to detect the importance, scale, and consistency of the causes of patchiness (Fasham, 1978).

Schooling of Adults

The adult northern anchovy is found in schools, but it is not known whether schooling is a necessary condition for survival. Mais (1974) reported several years of surveys with a sonar using the "sonar mapping" technique (Smith, 1970), which yields an estimate of the number of schools per unit area and an estimate of the distribution of school sizes. Table 2 is a summary of measured targets from all seasons in the California Dept. of Fish and Game Surveys (Mais, 1974). From this table it is seen that about 94 percent of all fish schools are less than 80 meters in diameter, but if school tonnage is proportional to school cross-sectional area, the 6 percent of schools larger than 80 meters in diameter contain more than half the anchovy biomass.

Seasonal data from Mais (1974), summarized in Table 3, show that the number and size of anchovy schools increase rapidly in summer and fall. There is reason to believe that the additional schools may contain radically less biomass (⅓ to ½) per unit surface area (Hewitt et al., 1976, Fig. 4b; Vent et al., 1976, Figs. 7d and 7e). These may not be spawning schools. Instead, they may be the large schools of loosely compacted juveniles spawned in the preceding fall, winter, and spring.

Anchovy schools are probably more compact in the daytime (when we have measured the schools with sonar) than they are at night when they are spawning. For example, the average daytime compactness of 15,000 grams of anchovy per square meter of school horizontal area (Hewitt et al., 1976) could have 7500 grams of female anchovy of which one-sixth (1250) are spawning; 380 eggs per gram of female would yield 475,000 eggs per square meter per night (Hunter and Goldberg, 1980). Our largest samples of eggs are about one-twentieth of this value, or 23,750 eggs per square meter. This value will have been influenced not only by the spawning school becoming less compact at night, but also by gross motion of the school during several (6–8) hours of spawning and by turbulent dispersion of the eggs following spawning and fertilization.

Spawning and schooling behavior in the Pacific sardine is probably analogous to that of the northern anchovy. A localized analysis of 183 plankton samples (from Smith and Richardson, 1977, p. 84) is shown in Table 4. The major features of the development of larval patchiness following spawning are shown. One characteristic is that there are 85 percent positive samples of first-feeding larvae (5 mm SL) and only 66 percent positive samples of first-day eggs. Owing to dispersion, more area appears to be covered by larvae than by eggs. In about three weeks, there have been increases in unit sample areas covered by 2, 8, 32, 128, and 512 sardines per 10 m^2 and decreases in areas with 0, 8, 192, and 32,768 sardines per 10 m^2. By the time the larvae are 10 mm long, there are no sample counts of 128 and above, and only 20 percent of the unit sample areas contain larvae.

Last, it should be noted that a condition of random distribution where the variance equals the mean is not attained in the set of data in Table 4. The variance:mean ratio is 11,840 to 1 for first-day eggs and is still 15 to 1 for 10 mm larvae. Unfortunately, we have insufficient observations to determine how much of the patchiness persists from the nocturnal spawning behavior of the adults and, alternately, how much of the larval distribution is the result of pattern-forming activities such as localized areas of high mortality, aggregation behavior of the larvae, and dynamic ocean events like convergence.

Statistical Consequences of Larval Patchiness

The primary statistical consequence of larval patchiness is the requirement for large numbers of samples to allow an estimate of absolute abundance with useful levels of precision. The number of samples required for a constant precision of ± 10% of the mean for the 3 days and sardine larvae to 10 mm length are shown at the bottom of Table 4. The range is from 6,759 samples of first-day eggs to 1,093 samples of 5 mm larvae. The rapid increase in samples with no larvae in the 8, 9, and 10 mm classes imposes additional sampling requirements.

Although the trends in sampling requirements by stage of development look reasonable, one should be cautious about the actual values, because the parameter estimates are sample estimates from only 183 samples. The actual number of samples required is a function of the population mean and the population variance, not the sample mean and variance. Current estimates of sample mean and variance are also likely to include sources of variance other than larval patchiness (English, 1964) such as temporal and spatial gradients

Table 2. Anchovy school diameter frequency distribution by school and biomass.

School diameter (m)	School biomass (metric tons)	Frequency	Sample proportions	Cumulative sample proportions	Class biomass (metric tons)	Biomass proportions	Cumulative biomass proportions
10	1.2	9,906	0.4338	0.4338	11,670	0.0274	0.0274
30	10.6	9,002	0.3942	0.8281	95,447	0.2245	0.2519
50	29.45	1,822	0.0798	0.9079	53,662	0.1262	0.3782
70	58	706	0.0309	0.9388	40,755	0.0959	0.4740
90	95	824	0.0361	0.9749	78,631	0.1849	0.6590
110	143	178	0.0078	0.9827	25,374	0.0597	0.7187
130	199	217	0.0095	0.9922	43,204	0.1016	0.8203
150	265	50	0.0022	0.9944	13,254	0.0312	0.8515
170	340	40	0.0018	0.9961	13,619	0.0320	0.8835
190	425	51	0.0022	0.9983	21,690	0.0510	0.9345
210	520	19	0.0008	0.9992	9,871	0.0232	0.9577
230	623	7	0.0003	0.9995	4,362	0.0103	0.9680
250	736	3	0.0001	0.9996	2,209	0.0052	0.9732
270	859	1	0.0000	0.9996	859	0.0020	0.9752
290	991	2	0.0001	0.9997	1,982	0.0047	0.9799
310	1,132	1	0.0000	0.9998	1,132	0.0027	0.9825
330	1,283	3	0.0001	0.9999	3,849	0.0091	0.9916
350	1,443	0	0.0000	0.9999	0	0.0000	0.9916
370	1,613	0	0.0000	0.9999	0	0.0000	0.9916
390	1,792	2	0.0001	1.0000	3,584	0.0084	1.0000

Table 3. Selected parameters of northern anchovy schools in California coastal waters (calculated from Mais, 1974).

Season	Anchovy schools (no/km^2)	Anchovy school size (m^2/school)	Coverage $\frac{\text{m}^2\text{ of anchovy school}}{\text{m}^2\text{ surveyed}}$
Winter	0.79	1151	0.0009
Spring	0.73	772	0.0006
Summer	1.22	1327	0.0016
Fall	1.98	1683	0.0033

(Colebrook, 1969) and regional and seasonal differences in abundance and survival. All data analyzed so far (Smith, 1972; Parker, 1980) indicate that the schooling pattern of the adults is the major source of variance.

Because schools are the major source of variance, any regional or seasonal correlative studies or analyses of variance must expend a high level of sampling effort to ascertain cause and effect of survival and environmental conditions. Log-transformation does not materially aid these comparisons. For example, in Table 4, the geometric mean provided by log-transformation increased from 23 stage "A" eggs to 40 5-mm larvae, while the arithmetic mean decreased from 673 stage "A" eggs to 161 5-mm larvae. It is mathematically possible to estimate the arithmetic mean from the mean and variance of log-transformed data, but there are insufficient studies to date to establish the efficacy of estimating two parameters, mean and variance of the log-transformed sample values, to further estimate another population parameter, the arithmetic mean. This statistical phenomenon should be explicitly solved by simulation before cause and effect studies are planned and conducted at sea.

It is apparent that the variance of numbers of eggs and larvae in samples is a result of the interaction of the size of the sample and the size of the patch. For example, patchiness on the scale of centimeters would not be measurable with a 1-meter net towed several meters. One obvious solution to sample variance would be to lengthen the tow until the proper proportion of larval patch to low-density areas between patches is obtained in a single sample. For this tactic to succeed there should be one scale of patch constant from place to place and from time to time.

It is not yet possible to test the consistency of patch scales; it is known that patchiness occurs on several broadly differing scales at sea. Smith (1970) reported a school group, believed to be northern anchovy, about 10 km in diameter. Fiedler (1978) reported the analysis of several school groups detected by California Dept. of Fish and Game Sea Surveys. The mode of school group radii detected was 8 miles (13 km) and the distribution ranged from 2 to 64 miles (3–100 km), with a log normal distribution with parameters $\overline{\ln x} = 2.319$ and variance 0.676. Within school groups, the number of schools per

Table 4. Sample frequency distribution of Pacific sardine eggs and larvae and number of samples required to obtain a standard error of the mean of 10% (modified from Table 3.17, Smith and Richardson, 1977).

		EGGS (Days post-spawning)			LARVAE (Standard length, mm)						
ln(X + 1)	X	A	B	C	3	5	6	7	8	9	10
0	0	65	44	76	29	27	38	57	91	124	146
1.1	2	7	14	5	13	5	12	23	21	32	23
2.2	8	14	14	16	36	20	32	51	52	19	12
3.5	32	20	27	31	50	46	68	45	18	8	2
4.9	128	36	33	17	29	49	30	7	1		
6.2	512	22	25	26	23	34	3				
7.6	2048	12	21	12	3	2					
9.0	8192	6	5								
10.4	32768	1									
	$\bar{X}$	673	557	225	129	161	43	15	6	3	1
	S_x	2,823	1,433	515	298	272	75	26	13	7	4
	S^2_x	7,968,421	2,054,393	264,757	88,524	73,756	5,574	668	170	46	15
Required samples to obtain standard error of mean =	$\frac{\bar{X}/1.96}{10}$	6,759	2,544	2,009	2,004	1,093	1,158	1,141	1,814	1,963	5,762
Percent positive		66	76	58	84	85	79	69	50	32	20

square mile exhibits a mode at 67 (20/km^2) and the distribution ranges from 9 schools to 221 schools per square mile (3–64/km^2). The log normal parameters are $\overline{\ln x} = 3.910$ and variance 0.510. School sizes exhibit a mode at 10 meters and a range of distribution of from 0 to 400 meters (Mais, 1974, Table 1). Also, the compaction of fish within the schools (Hewitt et al., 1976) varies from 0.25 to 64 kg/m2, with a mode of 4 kg/m^2 and a log-normal distribution with parameters $\overline{\ln x} = 1.952$ and variance 1.916. Graves (1977) photographed within fish schools at sea and detected a range of 50–366 fish per square cubic meter (Fig. 9). The underlying importance of the intensities and scales of contagion is that it is unlikely that a sample tow of any particular fixed length will diminish sample variance materially.

Biological Consequences of Larval Pattern

For fish schooled as adults, larval pattern may represent only a brief dispersed interlude in the life cycle. Some of the advantages of schooling as an adult could be conferred on the larval aggregations. Shaw (1978) lists the advantages of schooling as follows: conservation of energy while swimming through hydrodynamic interaction; enhanced reproductive opportunity; improved learning; greater tolerance of toxic substances; and protection from predators. Probably only improved learning and protection from predators would apply to the larval stage.

Protection from predators (Brock and Riffenburg, 1960; Hobson, 1978) through aggregation is implemented by decreased probability of contact and this is most advantageous when the size of the aggregation is adequate to satiate the predator. This latter consequence may operate at the larval stage or the maintenance of aggregations in the larval stage may only facilitate the formation of schools of "viable" size following metamorphosis into schooling juveniles.

Hewitt (1981) has considered the adaptiveness of larval pattern and described the life-cycle pattern through the larval stage for two fishes, the clupeiform anchovy (Engraulidae, *Engraulis mordax*), and the perciform jack mackerel (Carangidae, *Trachurus symmetricus*). He finds that the spawning pattern is less intense for the perciform. An index of patchiness indicates that the pattern becomes identical for anchovy and jack mackerel after two weeks of age.

Our interest in patchiness and particularly the changes in patchiness from one life stage to another stems from the conviction that since mean abundance of older larvae so far does not allow the distinction to be made between highly successful and moderately successful year classes, it may be that the intensity of pattern rather than mean abundance controls the success of survival in the later stages. With this rationale, the maintenance of patches in the larval state secures the advantages of schooling far sooner for the juveniles.

Lastly, patchiness may be a requirement for survival. Vlymen (1977)

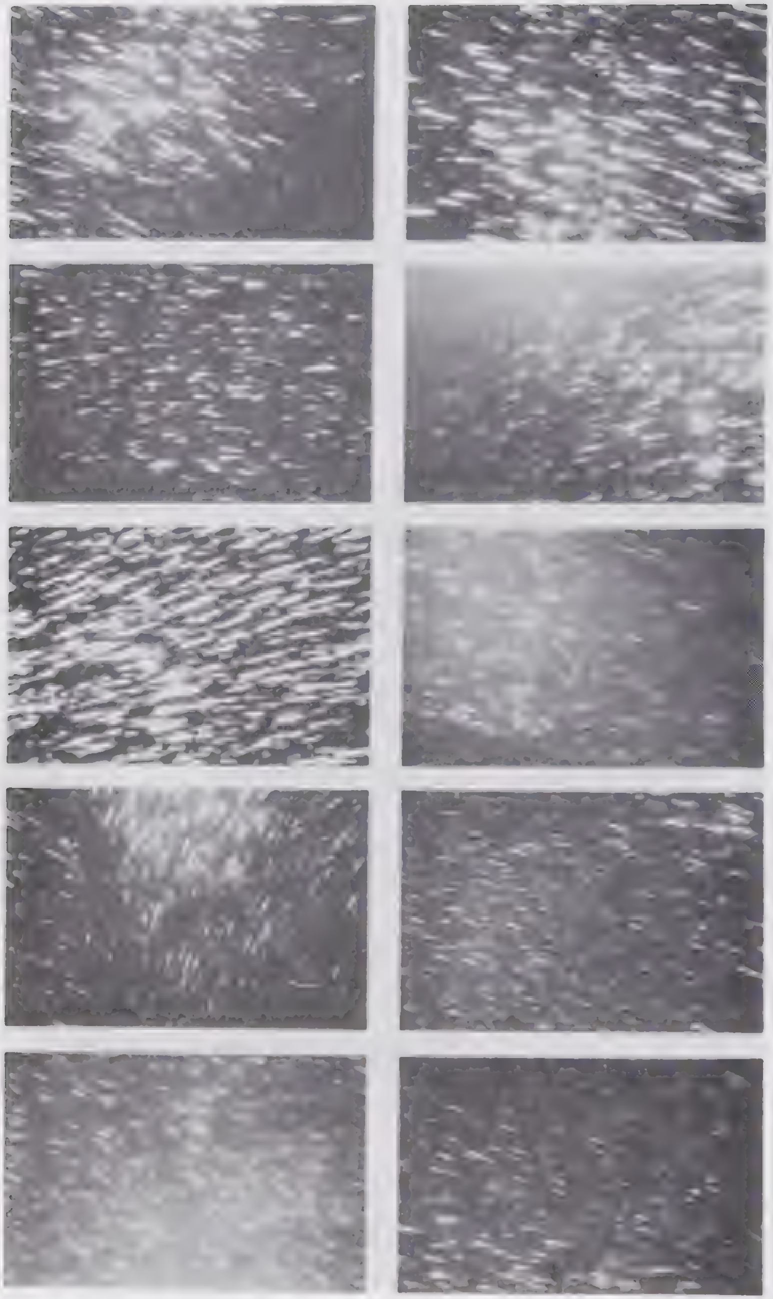

Figure 9. Portions of anchovy schools photographed at sea (Graves, 1977) with the Isaacs-Brown free vehicle drop camera. The mean of ten schools was estimated to be 115 fish per cubic meter (standard deviation 89, range 50–366, median 69).

demonstrated with a simulation model that larval growth requires patchiness in its food given the quantity of food in the sea. Thus a major oceanographic feature may be the stability to foster and maintain patches of food and permit the larvae to remain in favorable patches (Hunter, 1976; Lasker et al., 1970; Smith and Lasker, 1978; Lasker and Zweifel, 1978; Hewitt, 1981). Possibly one of the more enduring effects of the CalCOFI program has been the transition from regarding patchiness as a statistical nuisance to the appreciation of pattern as a necessity in the pelagic ecosystem.

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TIME SERIES OF ANCHOVY LARVA AND JUVENILE ABUNDANCE

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Good year-classes of anchovy, defined here as large contributors to catch, have been detected by the disproportionate entry of 0-group fish into the fishery. In a 9 year series of sea surveys (1969–77) conducted with a 15 m midwater trawl and sonar-mapping, the two best year-classes (1970, 1976) were characterized by the trawl catch of immediate post-larval fish in the spring of the year in which they were spawned. In a 12 year series (1966–77) the rank of a year-class contribution to the commercial catch and to the trawl catch agreed exactly in five cases, agreed within two ranks of twelve in six cases, and agreed as closely as four ranks in the remaining year.

Ahlstrom (1965) stated, "... we have found an unanticipated uniformity in the survival pattern of sardine and anchovy larvae from year to year." Since the data available then were the years 1951–59, I have examined the years 1951–75 to determine whether the estimates of the number of largest larvae sampled in the spawning biomass surveys foretold small and large year-classes of the central subpopulation of northern anchovy. Of the 9 years examined for immediate post-larvae in trawl surveys, only four (1966, 1969, 1972, 1975) had simultaneous ichthyoplankton spawning surveys. No larval surveys were conducted during the outstanding year-classes of 1970 and 1976. The year 1975 is classed as a failure by sea surveys and catch data: the 15 mm larva interpolation indicates a low abundance in spring. The projection of 15 mm larvae from embryonic and early larvae is also low in spring. Spring (April–June) is usually the major producer of 15 mm larvae. The 1972 year-class was moderate, but arose from a greater-than-usual abundance of 15 mm larvae in all seasons. The 1969 year-class was judged to be similarly moderate, but arose from less-than-usual abundance of 15 mm larvae. As in 1975, the 1966 year-class failed and also had a low abundance of 15 mm larvae.

A 21 year series (1951–69; 1972; 1975) of estimates of the abundance of 15 mm larvae and 0-group catch from bait and reduction fisheries from 1952 to 1977, and estimates of mortality rates in the embryonic, early, and late larval periods, has been compared with 0-group contribution to catch in the ensuing fishing season. There is a weak tendency (not significant at 5%) for embryonic (yolk sac) to early larval (9 mm) mortality rates to match year-class size. There is also a weak tendency for the abundance of 15 mm larvae to match year-class size. Exceptionally small recruitment can be seen from ichthyoplankton surveys, but moderate and large year-classes will not be discriminated by monitoring the first month of life of the northern anchovy.

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LARGE-SCALE ENVIRONMENTAL EVENTS ASSOCIATED WITH CHANGES IN THE MORTALITY RATE OF THE LARVAL NORTHERN ANCHOVY

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The larvae of the northern anchovy central subpopulation may be collected over 250 000 square miles of the northeast Pacific ocean. The spawning area is off central and southern California and northern Baja California and Mexico (Smith, 1978). Half of the larvae are normally concentrated in a 20 000 square mile area off southern California. In the late 1950's and early 1960's, the spawning area increased southward and offshore as the apparent biomass increased ten-fold.

Physiological data on the northern anchovy from the central stock indicate that they withstand colder temperatures than the Pacific sardine which occasionally inhabits the same spawning area. Thus, considerations of physiological tolerance relative to the sardine, upwelling of nutrient-rich water, and transport of plankton-rich water from the north would all tend to favor the survival of the northern anchovy in cold waters. This is not supported by the biological and physical oceanographic data now available. All of the onsets of apparent year-class failure to recruit to the fishable stock of northern anchovy; namely 1951, 1955, 1965, and 1974; have begun with abnormally cold seas. Persistence of the apparent year-class failure has been of the order 1 to 3 years.

Early larval mortality was found to be greater than 0.25 for 43% (46) of the region/quarter sets in the "bad" recruitment years, while only 27% of the region/quarter sets were characterized by this high mortality rate in the "good" recruitment years. No difference in mortality rate was noted for the late larvae in the same sets of years for the same region/quarter strata.

It appears that the best oceanographic indicator for larval anchovy "climate" is the January 30-m tempeature within the inshore and offshore regions of southern California and northern Baja California. The temperatures encountered are not near the lethal limit for larval anchovy, so that temperature is assumed to be merely an indicator of other oceanographic or biological events, such as transport from the subarctic water mass, deep mixing of the surface layer, upwelling, delayed embryonic development, or some combination. Twelve and 13° C temperatures at 30 m depth in the Los Angeles Bight appear to accompany poor recruitment while temperatures of 14° to 16° C appear to favor moderate or high recruitment.

The mechanism or mechanisms leading to poor recruitment are not known, but events at the yolk-sac larval stage are implicated in certain extremely cold years.

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FIVE

Reexamination of the Life Table for Northern Fur Seals with Implications about Population Regulatory Mechanisms

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TOM POLACHECK

INTRODUCTION

Fur seal *(Callorhinus ursinus)* populations in the north Pacific have periodically been subjected to intensvie harvesting since the 1700s (Lander and Kajimura, 1976). Several breeding areas are currently used, with apparent segregation of the animals into separate breeding populations (Kenyon et al., 1954). The best known of these populations is that occupying the Pribilof Islands in the Bering Sea. This population has been the subject of intensive scientific study and harvest management since 1911, as a result of a treaty between Japan, Canada, U.S.S.R., and the United States (Roppel and Davey, 1965). The population was at an extreme low point in abundance in 1911, when only about 70,000 pups were born annually. Following 1911 the population increased, and currently approximately 300,000 pups are born annually (Lander and Kajimura, 1976). The fur seals occupy beaches on the Pribilof Islands during the summer months, where pupping and breeding occur. Males establish and defend harems. Initially the treaty terminated all harvesting, but since 1918 a large proportion of the males between the ages of 2 and 6 have been harvested each year under the assumption that they are "surplus" in the sense that they are not necessary for the maintenance of the population.

A series of studies since 1954 (Kenyon et al., 1954; Scheffer, 1955; Nagasaki, 1961; Chapman, 1961, 1964, 1973) have described, elaborated on, and tested the hypothesis that this population is regulated in size by density through changes in the survival rate of young animals (see also Chapter 10). In addition, a lesser number of studies (Ichihara, 1971; Bulgakova, 1971) have tested this same hypothesis for breeding populations in the western Pacific Ocean. These studies are based on results of research programs by the treaty nations.

In this chapter we review the available information on reproductive and survival rates of Alaska fur seals in the late 1950s, when the population was thought to be in equilibrium, and present a life table for the population for this period. Noting that the population was apparently increasing at about 8%/year when it was at low abundance (see Chapter 10), we calculate the nature and magnitude of changes in the life table implied in the general density-dependent hypothesis.

This examination of the implied changes in the life table was suggested by our review of the hypothesis that vital rates are changing in response to population density (Smith and Polacheck, 1981). We found that in most cases the available data do not support the general hypothesis of density-dependent changes. Furthermore, even if the changes suggested in earlier interpretations of the data are real, the magnitude of these changes is insufficient to account for the high rate of increase in population size observed during the early part of this century. Thus, one objective of this chapter is to determine the magnitude of the changes in vital rates that we would expect given this high rate of increase. We then consider if the absence of evidence for such change is reasonable in view of the quantity of data that have been collected.

The information available for the Pribilof Island fur seal herd is most complete for St. Paul Island, where approximately 80% of pups are born each year. Because information from St. George Island is less complete, whenever possible we will consider only the St. Paul data, although parallel trends have been observed on both islands.

BACKGROUND

The data for this work come from the commercial harvest of 2 to 6-year-old males (Figure 1) and from the national scientific research programs. The research programs have fluctuated widely in scope and have encompassed many aspects of the biology of fur seals. The principal information from these programs relevant to this Chapter are (1) the counts of pups born from 1911 to

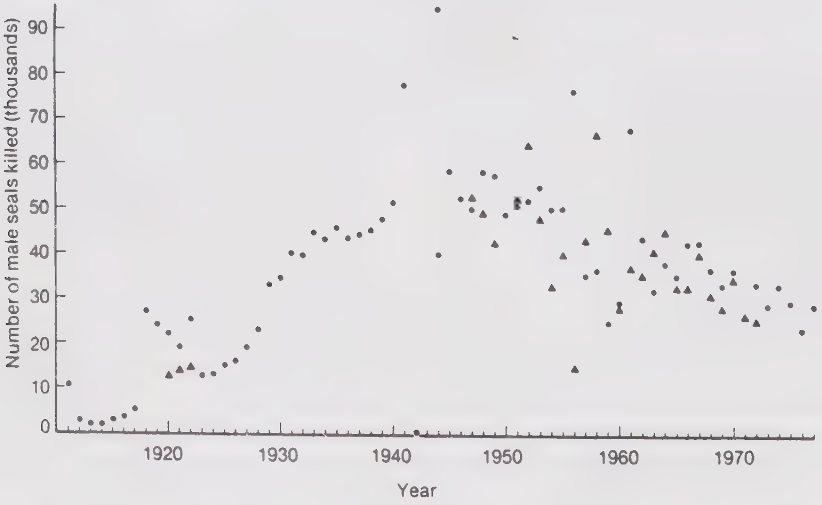

Figure 1 Number of male seals killed on St. Paul Island in the annual harvests, by year (●) and by year class (▲), from NPFSC (1961, 1969, 1971, 1975) and NMFS (1978).

1924, (2) the counts of harem and idle bulls since 1911, (3) the determination of the age of the kill of males from tooth layers since 1947, (4) the pelagic samples of seals from 1958 to 1961, (5) the estimates of numbers of pups born since 1961, and (6) the numbers of pups found dead on the beaches each summer since 1911. These data are described in detail in Smith and Polacheck (1981), and in papers referenced therein. A brief description of the use we make of each of these sources of data follows.

Direct counts of pups on rookeries were made from 1911 to 1924, varying from counts on all rookeries to counts on a sample of the rookeries. Useful estimates or counts are available only for the years shown in Figure 2.

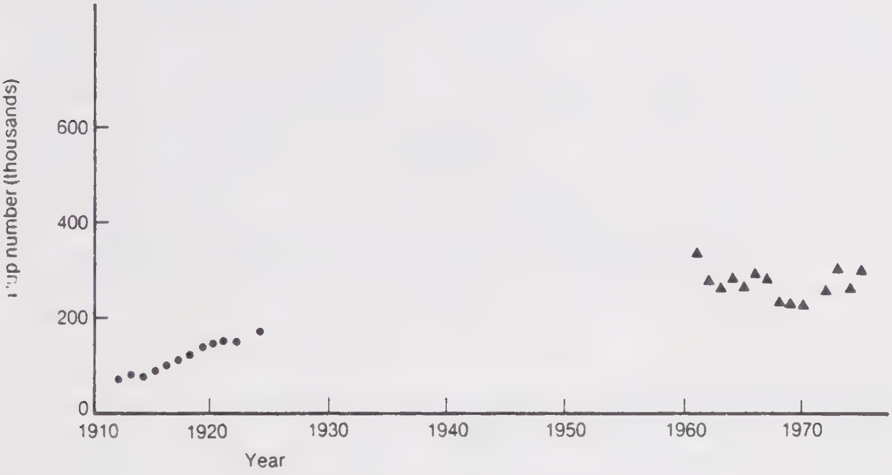

Figure 2 Counts (●) and estimates (▲) of the number of pups born on St. Paul Island, from Lander and Kajimura (1976).

The numbers of adult males on the rookeries, by reproductive class, have been estimated each year since 1912 (Figure 3). The most reliable data are available for the number of males actually holding harems, termed "harem masters." Fewer accurate data are also recorded for the number of adult males not holding harems, termed "idle bulls." The changes in abundance of harem and idle males provide the only measure of the numbers of males escaping the harvest, although uncertainties about survival rates make this difficult to interpret quantitatively.

The determination of age is accomplished by counting ridges on the surface of the teeth (Scheffer, 1955) and by counting layers inside the teeth (Anas, 1970). Age has been determined using these methods for a sample of the animals killed in the harvest since 1947. This permits estimation of the total numbers of males killed from each class, providing estimations of year class strength of males for ages 2 to 6. The estimates of total male kill by year class since 1947 are shown along with the annual kills of males in Figure 1.

From 1958 to 1974, age and reproductive condition were determined for females collected pelagically. Samples of reasonable size were obtained by U.S. researchers from 1958 to 1961 and are used here to estimate reproductive and survival rates.

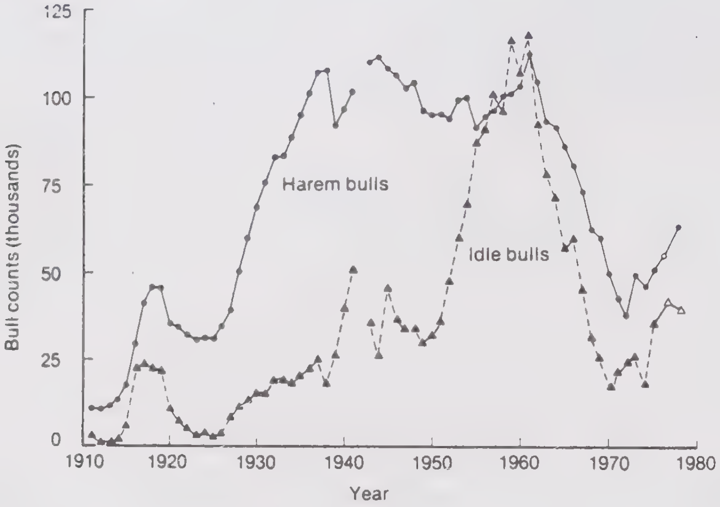

Figure 3 Counts of harem and idle bulls for St. Paul Island, from 1911 to 1977, from Lander and Kajimura (1976) and NMFS (1978).

Starting in the late 1940s pups were tagged in an attempt to estimate the number of pups born. Recovery information was based on the subsequent kill of males at ages 2 through 6. The estimates obtained from this procedure are not considered to be reliable (Chapman, 1964). Starting in 1961, estimates of the numbers of pups born were made based on marking pups by shearing a patch of fur, and subsequently recovering marked individuals in the same summer (Chapman and Johnson, 1968). These latter estimates are considered reliable and are shown in Figure 2 along with the earlier counts of pups born.

The number of pups found dead on the beaches prior to their leaving land in late summer had been estimated for a number of years since 1911. These counts are thought to represent nearly all the mortality occuring on land. They are useful in determining if the survival of pups on land has changed with increased population.

In analyzing these data we use standard statistical procedures for significance tests (Snedecor and Cochran, 1967) and follow Seber (1973) for estimating survival rates. In addition, we make use of discrete life-table analyses, following Mertz (1971) and Leslie (1945).

FEMALE SURVIVAL RATES

Previous Estimates

Survival rates of adult females have been estimated variously, based primarily on the age composition of pelagic samples taken in 1952 and from 1958 to 1961. Chapman (1961) estimated an average rate of 0.79 (rounded to 0.80) based on the age composition of the 1958-1960 U.S. pelagic samples. Nagasaki (1961) analyzed the pelagic samples from the United States for 1958, from the Japanese research program for 1952 and 1958, and the age structure of the females harvested on the Pribilof Islands in 1956 and 1957. He concluded that the sampling biases were such that". . . it is almost impossible, in the present state of study, to calculate accurate mortality rate by age based on the observed age-composition of catches". Chapman (1964) analyzed the U.S. pelagic samples for the years 1958 to 1961 combined, and estimated age-specific survival rates as the ratios of the "adjusted" numbers of each successive pair of ages. The "adjusted" numbers were obtained by fitting a Gompertz curve to the observed age distribution for seals at age 8 and older. This had the effect of smoothing the data and allowing extrapolation along this curve to ages less than 8. However, the fit of the smoothing curve to the observed numbers at each age is not very good with a systematic overestimation of the observed numbers sampled for ages 8 to 15.

Evidence for the Stationarity of the Age Structure

The age distribution of the female seals collected in the pelagic samples by U.S. research vessels is given in Table 1. In order to obtain unbiased estimates of survival rates, the age distribution of the female fur seal population must be stationary (i.e., constant size for the population and with constant proportions in each age class), and the sampling must be representative across the age classes for which survival estimates are made. General demographic theory states that if the population has been at a constant size for a certain period of time, the age structure will approach constant proportions from year to year.

It appears that the population probably reached a maximal, and perhaps constant, size in this century during the late 1940s and early 1950s. This is suggested by (1) the relatively constant annual kill of males between 1944 and 1955, (2) the declining rate of increase in the annual kills between 1930 and 1944, (3) the relatively constant counts of harem master bulls between about 1938 and 1961, and (4) the relatively constant counts of idle males between 1943 and 1951. These are all measures of the male segment of the population, but they suggest that the female segment was likewise relatively constant in size. The harvesting practices were relatively stable from the early 1920s until the early 1950s (Roppel and Davey, 1965).

The conclusion of an approximate constant size is brought into doubt by data for the kill from each year class, which are available since 1947 (Figure 1). The fluctuations in these numbers suggest that the number of seals at ages 2 to 5 in successive year classes varied considerably during this period; this might induce nonstationarity in the age distribution. The fluctuations in the kill by year class in the 1950s are also reflected in the annual kills of males (Figure 1). Similar variations in the annual kills are not seen prior to 1956 (disregarding the war years), which suggests that year class strength may not have affected age structure stationarity prior to the 1950s. Moreover, whereas the numbers killed by year class from 1947 to 1953 are consistent with the hypothesis of constant size, the data from 1954 and 1971 suggest a general but variable decline. It should be noted that the harvesting regime for males changed somewhat starting in the mid- to late 1950s as the annual catches began to decline (Roppel and Davey, 1965). However, these changes do not seem to explain the decline. This apparent decline, if real, should not have affected the age structure for the older animals between 1958 and 1961.

Table 1 Number of Female Seals by Age Class Collected by U.S. Researchers, by Year

Age	1958	1959	1960	1961	1958-1961
3	39	43	18	84	184
4	42	93	36	96	267
5	70	114	55	68	307
6	99	118	45	62	324
7	103	143	66	95	407
8	102	164	105	107	478
9	81	108	144	114	447
10	97	96	129	112	434
11	113	98	136	82	429
12	134	76	106	71	387
13	110	56	120	76	362
14	92	70	107	67	336
15	71	87	67	68	293
16	56	69	53	55	233
17	36	36	46	24	142
18	22	27	23	25	97
19	14	16	19	10	59
20-22	5	17	12	9	43

By 1958, when the first pelagic samples used here were taken, any irregularities in the age structure caused by the increase in size of the population since 1911 should have diminished to inconsequential levels if the population had approached a constant size. This was checked and confirmed by examination of the predicted age structures from a simulation model of population size. This model, described by Smith and Polacheck (1981), is structured around single-species density-dependent concepts. It assumes variously that fecundity, juvenile survival, and adult survival change with density such that the model mimics the observed growth of the population as reflected in the male harvest and, where available, the numbers of pups born. There are slight biases toward understimation in survival rates calculated from such simulated age structures for the late 1950s.

An additional complication in the representativeness of the pelagic samples is that substantial numbers of females of several age classes were killed beginning in 1956, in a management effort to reduce the numbers of pups born and thereby increase the survival of pups to age 3. The effect on the age structure of this harvesting was explored by further examination of the simulation model described above. The calculations were extended through 1961 with the age structure of the harvest of females from 1956 to 1961 incorporated into the model. The simulated age structures suggest that no effect of this harvest would have been observable for animals age 11 and older through 1961. Furthermore, the age structure probably did not show any effect of this harvesting for animals older than 8 in 1958, 9 in 1959, and 10 in 1960. The lack of effects for these ages is attributable to a combination of the magnitude and age structure of the female harvest.

New Estimates

Inspection of the data in Table 1 demonstrates that the samples are not representative of the animals in the younger ages as the proportions in each age class in the harvest show an increase with age up to the ages of 7 to 9 in all four years. There is considerable variability in the proportions observed in the age groups older than 8, however, which suggests the possible nonrepresentativeness of the samples between years. Following Seber (1973), the equality of the observed proportions between years within ages was tested with a chi-squared statistic. The test statistic for the data in Table 1 has a value of 122, with 36 degrees of freedom. As this is large ($p < 0.001$), there are likely some changes between years in the proportions within each age class. This could be the result of sampling biases between years or of nonstationarity of the age distribution.

The questions of the representativeness of the samples between years and the possibility of sample biases within years over the geographic areas sampled (Nagasaki, 1961) need to be investigated further. As the data are not readily available in a form that will allow such investigation at this time, and as these data have been used in the past (Chapman, 1961) to estimate survival rates, we have used them as presented, recognizing the need for more detailed investigation in order to better evaluate our results.

Owing to apparently changing survival rates with age, the most adequate estimator for survival for each age class is the ratio of numbers sampled at successive ages (Seber, 1973). Such estimates have not been presented elsewhere for the U.S. data, and are given here by year (Table 2) along with appropriate descriptive statistics (Seber, 1973). It is clear on inspection that the variability of the estimates increases markedly after approximately age 16, and that the samples are subject to high levels of variance in that they occasionally yield

Table 2 Survival (S) as Ratios of Observed Numbers of Females of Successive Ages in U.S. Pelagic Samples for Ages 8 to 20 by Year[a]

Age	S	$\hat{\sigma}$	C	r
		1958		
8	0.79	0.092	−0.0117	−0.55
9	1.20	0.680	−0.0144	−0.50
10	1.17	0.161	−0.0122	−0.50
11	1.19	0.152	−0.0073	−0.45
12	0.82	0.106	−0.0062	−0.50
13	0.84	0.118	−0.0070	−0.49
14	0.77	0.122	−0.0086	−0.50
15	0.79	0.141	−0.0091	−0.47
16	0.64	0.137	−0.0091	−.048
17	0.61	0.165	−0.0177	−0.49
18	0.64	0.218	−0.0097	−0.33
19	0.21	0.136	−0.0238	−0.45
20	0.33	0.385	—	—
		1959		
8	0.66	0.067	−0.0054	−0.53
9	0.89	0.125	−0.0095	−0.52
10	1.02	0.147	−0.0081	−0.47
11	0.78	0.119	−0.0075	−0.49
12	0.74	0.130	−0.0164	−0.57
13	1.25	0.224	−0.0222	−0.50
14	1.24	0.200	−0.0113	−0.44
15	0.79	0.128	−0.0060	−0.44
16	0.52	0.107	−0.0109	−0.53
17	0.75	0.191	−0.0165	−0.46
18	0.59	0.187	−0.0116	−0.39
19	0.31	0.160	−0.0875	−0.67
20	1.40	0.820	—	—
		1960		
8	1.37	0.122	−0.0092	−0.45
9	0.90	0.109	−0.0064	−0.52
10	1.05	0.130	−0.0077	−0.46
11	0.88	0.101	−0.0131	−0.55
12	1.13	0.151	−0.0124	−0.47
13	0.89	0.119	−0.0134	−0.45
14	0.63	0.098	−0.0121	−0.52
15	0.79	0.145	−0.0064	−0.51
16	0.87	0.175	−0.0189	−0.42
17	0.50	0.128	−0.0167	−0.55
18	0.83	0.256	−0.0280	−0.36
19	0.32	0.148	−0.0286	−0.62
20	1.00	0.578	—	—

Table 2 (continued)

Age	$\hat{S}$	$\hat{\sigma}$	C	r
		1961		
8	1.07	0.107	−0.0085	−0.49
9	0.98	0.131	−0.0073	−0.46
10	0.73	0.106	−0.0060	−0.52
11	0.87	0.140	−0.0083	−0.53
12	1.07	0.177	−0.0084	−0.48
13	0.88	0.148	−0.0052	−0.52
14	1.02	0.175	−0.0074	−0.47
15	0.81	0.147	−0.0130	−0.41
16	0.44	0.107	−0.0094	−0.60
17	1.04	0.298	−0.0180	−0.37
18	0.40	0.150	−0.0137	−0.54
19	0.70	0.345	−0.0526	−0.36
20	0.29	0.229	—	—

[a] Also given are the estimated standard deviations ($\hat{\sigma}$) for early estimates, and covariances *(C)* and correlation coefficients *(r)* of successive pairs of estimates.

estimates greater than one. The estimates that are greater than one are not limited to those ages where the female kill might have had an effect.

The pairs of estimates of survival rates for successive age classes are negatively correlated, with the correlation coefficient depending only on the actual values of the survival rates for those ages. An expression for the correlation coefficient *(r)* in terms of the two annual survivals (S_x, S_{x+1} for ages x and $x + 1$) can be obtained by simplifying the expression for the correlation coefficient in terms of the covariance and the variances, as given in Seber (1973), obtaining

$$r(S_x, S_{x+1}) = -[(1 + S_x)(1 + S_{x+1}^{-1})]^{-1/2}$$

The magnitude of the second survival rate in a pair has more of an effect on the value of the correlation than does the magnitude of the first, and the correlation cannot exceed 0.7 in absolute value. Also for the survival rates in the neighborhood of those estimated for fur seals, the correlation coefficient will be around −0.5. The covariances and the corresponding correlations between pairs of estimates are given in Table 2.

The average across years of the estimated survival rates in Table 2, weighted inversely by their variances, are given in Table 3 (S), along with Chapman's (1964) estimates of survival rates S_c for these ages, for comparison. Note that the weighted average estimates are generally greater than Chapman's from ages 9 to 15, and lower from ages 16 to 19. These average estimates are shown in Figure 4.

These estimates of the survival rate are probably reliable for ages 12 and older. The estimates for ages 8 to 11 must be used with considerably less confidence owing to possible effects of the female harvest. We have little informa-

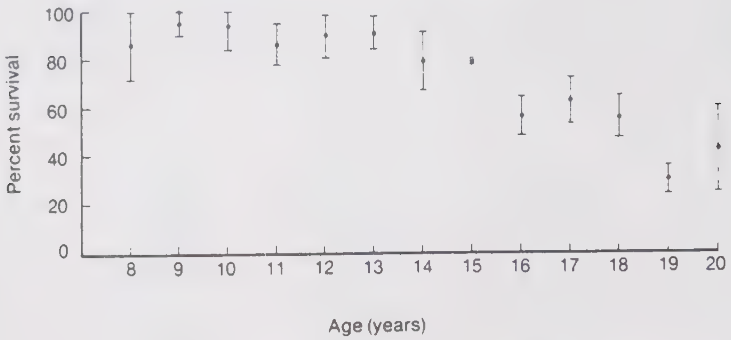

Figure 4 Estimates of annual survival rates by age with associated ranges of plus and minus one standard deviation, from Table 3.

tion on the survival rates for animals younger than 8 because of the apparent nonrepresentativeness of the sampling for these ages. Chapman's (1961) estimates of survival for ages 3 to 7 are very uncertain because of the lack of useful data for these ages and the poor fit of the Gompertz equation he used for extrapolation.

Table 3 Survival Rate Estimates for Female Alaska Fur Seals Pooled Across Years From Table 2 *(S)* and from Chapman (1964)$(S_c)^a$

Age	S	S_c
8	0.86 (0.144)	0.91
9	0.95 (0.058)	0.90
10	0.94 (0.099)	0.88
11	0.86 (0.085)	0.86
12	0.90 (0.090)	0.84
13	0.91 (0.066)	0.81
14	0.79 (0.118)	0.77
15	0.80 (0.004)	0.74
16	0.56 (0.080)	0.69
17	0.63 (0.091)	0.64
18	0.56 (0.085)	0.57
19	0.30 (0.063)	0.50
20	0.42 (0.177)	0.41

[a]Standard deviations in parentheses.

REPRODUCTIVE RATES

Previous Estimates

The pelagic samples of female seals (1958-1974) provide the basic data for estimating reproductive rates. The seals reproduce annually on the breeding islands, mate immediately after parturition, and have delayed implantation of the ovum. The females collected pelagically are classified as pregnant or nonpregnant on the basis of a detailed examination of the reproductive tract.

Chapman (1961) examined the proportion pregnant for the 1958, 1959, and 1960 samples. Utilizing his estimates of the age-specific mortality rates as discussed above, Chapman estimated the average pregnancy rate for seals 3 years of age and older at 0.60 (i.e., for a population with a stable age distribution, 60% of the females aged 3 and older are estimated to give birth each year). Nagasaki (1961) analyzed a mixture of pelagic and land-based samples for pregnancy rates. He concluded that there were differences in the pregnancy rate between the Japanese and U.S. pelagic samples for the younger ages, and that the land-based samples suffered consistent biases in the representativeness of reproductive condition. (Nagasaki's precise estimates are not tabulated, but are shown in his Figure 8.) Chapman (1964) further analyzed the pelagic samples from 1952, and 1958 to 1961 combined, for both U.S. and Japanese researchers. He also noted the difference between the U.S. and Japanese samples and concluded that his previous estimate of 0.60 for the Pribilof seals is the most reasonable.

Revised Reproductive Rate Estimates

The published analyses of pregnancy rates do not exhibit all the age-specific values (except perhaps Nagasaki's untabulated values). Also, the variability associated with these estimates is not given. We have calculated the values by year with their standard deviations (Table 4). The standard deviations are obtained by assuming binomial sampling within an age class (i.e., $\hat{\sigma}(P) = (p(1 - p)/n)^{1/2}$, where p denotes the estimated proportion pregnant and n denotes the number samples of that age). Combined age-specific pregnancy rates over the four years are also given as the average of the annual estimates weighted inversely with their variances. The averaged pregnancy rates from Table 4 are shown in Figure 5. Useful samples for pregnancy rates are available for years beyond 1961. These are not included in order to be consistent with the data from which survival rates were estimated above, but they do not affect the general conclusions of this chapter. These samples are discussed further in Smith and Polacheck (1981).

The problems of bias apparent in estimating survival from the pelagic samples are not as important in estimating pregnancy rates. For unbiased estimates in this regard females of any particular age must be equally likely to be in the sample, regardless of reproductive condition. The estimates of pregnancy rate by age are consistent over the four years shown in Table 4 and are similarly consistent for the data from 1962 to 1970 for females older than 5 years of age. There is some evidence of a declining pregnancy rate for ages 3, 4, and 5, between 1962 and 1970, but the changes are neither large nor consistent and may represent sampling variability and sampling area differences (A. Johnson, personal communication).

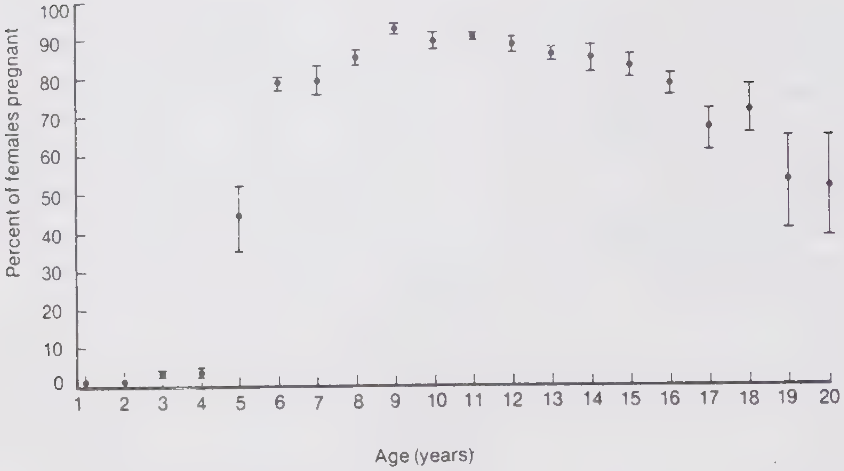

Figure 5 Estimates of annual reproductive rates as percent pregnant, by age, with associated intervals of plus and minus one standard deviation from Table 4.

SURVIVAL DURING THE FIRST SUMMER

The annual counts of dead pups can be compared to the estimates of numbers of pups born to get estimates of survival to the time the pups leave the islands at the end of summer. These data, up to 1951, have been analyzed by Kenyon et al. (1954), where it is noted that the estimated mortality rates had increased substantially just prior to 1951 and that this increase was associated with an apparent large increase in population size. Nagasaki (1961) presented an analysis of much the same data and also concludes that a density-dependent relationship was involved. However, the estimates of the number of pups born since 1924 used in both papers have subsequently been considered unreliable (see above and Chapman, 1964).

The same type of analysis has been extended up to 1976 using estimates of numbers of pups born from shearing and recapture estimates (Smith and Polacheck, 1981). In that analysis, the survival of pups to the end of the summer exhibits a decline with increased population size. This decline is apparent in the estimates of first summer survival in Table 5, which are calculated from data in Smith and Polacheck (1981, Table 3 of Appendix I in that reference).

Table 4 Proportion of Pregnant Female Seals by Age and Year of Sample $(\hat{p})$ and Weighted Average Proportion of Pregnant Over All Years $(\bar{p})^a$

	1958		1959		1960		1961		Average	
Age	$\hat{p}$	$\hat{\sigma}(\hat{p})$	$\hat{p}$	$\hat{\sigma}(\hat{p})$	$\hat{p}$	$\hat{\sigma}(\hat{p})$	$\hat{p}$	$\hat{\sigma}(\hat{p})$	p	$\hat{\sigma}(\bar{p})$
3	0.03	0.025	0	0	0	0	0	0	0.03	0.008
4	0.02	0.024	0.06	0.025	0.03	0.027	0.01	0.010	0.03	0.009
5	0.46	0.060	0.56	0.046	0.49	0.067	0.21	0.049	0.44	0.084
6	0.81	0.040	0.77	0.039	0.80	0.060	0.76	0.054	0.79	0.012
7	0.89	0.030	0.76	0.036	0.79	0.050	0.76	0.044	0.79	0.035
8	0.89	0.031	0.87	0.027	0.86	0.034	0.79	0.039	0.85	0.019
9	0.96	0.021	0.89	0.030	0.92	0.022	0.94	0.023	0.92	0.014
10	0.88	0.033	0.85	0.036	0.92	0.025	0.94	0.023	0.89	0.019
11	0.92	0.026	0.90	0.031	0.91	0.024	0.89	0.035	0.90	0.006
12	0.82	0.033	0.88	0.037	0.91	0.028	0.43	0.030	0.88	0.024
13	0.83	0.036	0.89	0.041	0.88	0.030	0.83	0.043	0.86	0.015
14	0.82	0.040	0.84	0.043	0.80	0.038	0.93	0.032	0.84	0.032
15	0.79	0.048	0.89	0.034	0.84	0.045	0.79	0.049	0.82	0.025
16	0.79	0.055	0.75	0.052	0.72	0.062	0.86	0.047	0.78	0.031
17	0.57	0.083	0.81	0.066	0.67	0.069	0.63	0.099	0.66	0.053
18	0.59	0.105	0.85	0.068	0.83	0.079	0.64	0.096	0.71	0.062
19	0.29	0.121	0.81	0.097	0.58	0.113	0.50	0.158	0.53	0.115
20	0.40	0.219	0.59	0.119	0.33	0.136	0.89	0.105	0.51	0.131

[a] $\hat{\sigma}(\bar{p})$ indicates standard deviations.

SURVIVAL TO AGE 3

Several estimates of the survival of younger seals are given in the literature (Chapman, 1961, 1964, 1973). This has been an area of great interest and research, since the primary hypothesis for the natural regulation of fur seal populations has been that the survival of younger animals varies with population size. Unfortunately, most of the data available to estimate juvenile survival rates are not easy to interpret. Certain key observations are missing in some critical years, and vital rates that would permit estimation of the missing information from other information are poorly known.

The basic technique used to estimate the survival rate for this period is to divide the number of male seals born into the sum of the male seals harvested and escaping harvest. The number escaping has not been reliably estimated. These estimates are discussed in Smith and Polacheck (1981), where it is concluded that reliable estimates of survival rates for these ages are not available.

In the absence of estimates of the actual survival rates, the ratio of the male kills from each year class and the estimates of pups born provide a lower bound to the actual survival rates. The available data are shown in Table 5, with the corresponding estimated lower bounds. Values are not presented for the 1950s because of the problems associated with the estimates of numbers of pups born during this period. Also included in Table 5 are estimated lower bounds for their survival from 1920 to 1922. These estimates are also based on the ratio of the actual kill of males from each year class to the estimated number of pups born. However, in this case, the actual kill from each year class was estimated from the size-frequency distribution of the male kill and may contain larger biases.

The average of these estimates of lower bounds for the survival rates for the years 1920 to 1922 (0.21) is significantly different from the average for the years 1961 to 1970 (0.26), but the difference is not in the expected direction. However, it is not clear that these lower bounds are comparable, since the number of males surviving the harvest at age 4, which is the primary factor causing these numbers to be less than the true survival rates, has presumable changed significantly with changing harvesting procedures (Roppel and Davey, 1965).

These lower bounds for the survival from birth to age 3 can be adjusted to the period from the end of the first summer to age 3 by dividing by the estimated first summer's survival rates indicated in Table 5. This adjustment serves to increase the difference between the two periods, although the latter period (when populations were higher), continues to have higher estimated lower bounds of survival rates.

We have explored in detail the general problem of estimating the survival rate of male seals from the annual kills and the annual counts of harem and idle bulls in Smith and Polacheck (1981). Calculations in that report suggest that the available information is consistent with a wide range of values of juvenile survival, but that a maximum value may be about 72%. This may be considered a minimal upper bound for the juvenile survival rate.

EQUILIBRIUM RATES

If available estimates of survival and pregnancy rates are asssumed to be for a period of time when the population was not markedly changing in size, the net rate of change should have been approximately zero. Making this assumption and ignoring any possible bias that would result from nonrandom sampling, we have estimates of pregnancy rates for all age classes, of survival rates for females ages 12 and older, and of survival rates for both sexes during the first summer of life. In addition, we have some estimates of lower bounds for survival of males from birth to age 3. We have no direct estimates of survival from ages 3 to 8, and some possibly biased estimates of survival from ages 8 to 12. The existing estimates can be used to calculate estimates for those values of survival rates for which we have little or no information and which are consistent with a population growth rate of zero.

Using standard life-table calculations, we computed the rate of survival of females between birth and age 3 that would result in a zero net rate of increase. This was done for a range of values of survival rates from ages 3 to 23 and for ranges of estimates of pregnancy rates and survival rates of older females consistent with the variances of the above estimates. The results are shown in Table 6.

Table 5 Estimated Number of Pups Born and Subsequent Harvest of Males from that Year Class on St. Paul Island, and Estimated Survival over the First Summer

	Pups Born[a] × 1000	Kill of Males[b]	Survival to Age 3[c]	First Summer's Survival Rate[d]
1920	143	14,751	0.206	0.972
1921	150	15,375	0.205	0.973
1922	159	17,050	0.215	0.983
1961	337	36,882	0.219	0.820
1962	278	34,991	0.252	0.829
1963	264	40,126	0.304	0.870
1964	285	44,882	0.315	0.920
1965	267	32,202	0.241	0.846
1966	296	32,285	0.219	0.924
1967	284	39,504	0.278	0.948
1968	235	30,266	0.258	0.887
1969	234	27,778	0.237	0.940
1970	230	34,188	0.297	0.906

[a] 1920 to 1922 from Chapman (1961, his Table 2); 1961-1970 from Lander and Kajimura (1976, their Table 2).

[b] 1920 to 1922 from Chapman (1961, his Table 3) as the sum of commercial and native kills; 1961-1970 from Lander and Kajimura (1976, their Table 6); 1970 from Marine Mammal Division (1977).

[c] Lower bound, assuming all kill was at age 3.

[d] Calculated from Smith and Polacheck (1981, Table 3 of Appendix I), for those years where the kill of males is known.

Table 6 The Calculated Survival Rates from Birth to Age 3 that Result in a Net Rate of Increase of Zero, Using Combinations of Ranges of Other Survival Rates and Pregnancy Rates

	Pregnancy Rates			
Survival Rates for Older Animals	$S_{3,4}$[a]	Low	Central	High
Low	0.80	0.90	0.85	0.81
	0.85	0.71	0.68	0.65
	0.90	0.57	0.55	0.52
	0.95	0.46	0.44	0.42
Central	0.80	0.71	0.68	0.65
	0.85	0.56	0.54	0.51
	0.90	0.45	0.43	0.41
	0.95	0.36	0.34	0.33
High	0.80	0.54	0.51	0.49
	0.85	0.42	0.40	0.39
	0.90	0.33	0.32	0.31
	0.95	0.27	0.25	0.24

[a] $S_{3,4}$ is the survival from ages 3 to 4.

The survival rates used between ages 3 and 12 were constructed by linear interpolation between the estimated value at age 12 and a range of values at age 3, as shown in Figure 6. The ranges of values for the pregnancy rate and the survival rate of older animals used in the computations in Table 6 were constructed as the weighted average estimates given in Tables 3 and 4 and these estimates plus (high) and minus (low) one standard error. These ranges of survival and pregnancy rates are not meant to represent confidence intervals, as discussed above, but rather to serve as a basis for considering the ranges of values of survival from birth to age 3 consistent with a zero rate of increase of the population.

It can be seen from Table 6 that within the range of uncertainty of the parameter estimates, allowable values of survival from birth to age 3 are generally higher than the lower bounds for this rate given in Table 5. To get values as low as the average estimated lower bounds from 1961 to 1970 (0.26) one must have rather high survival rates for all ages. Moreover, the lowest estimates of the adult survival rates tend to give biologically unreasonable estimates of the survival rates from birth to age 3. It can also be seen that within the sampling variability of the estimates of pregnancy and survival rates the calculations are rather more sensitive to changes in survival rates than to changes in pregnancy rates.

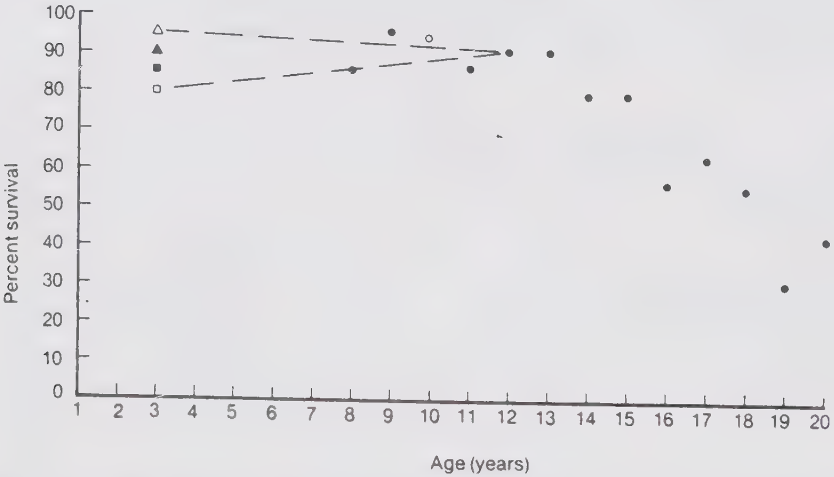

Figure 6 Survival estimates used in life-table calculations, and the method of interpolating values (dashed lines) between age 3 and 12. See text for details.

MAXIMUM POPULATION GROWTH RATES

While it is apparent that there are many uncertainties in our understanding of the reproductive and survival rates for Alaska fur seals when the population was at equilibrium, it is still possible to usefully address the question of what these rates would have had to have been when the population was increasing. The counts of pups made from 1912 to 1924 provide our best estimate of how fast the population is capable of increasing. This was about 8%/year (see Eberhardt, Chapter 10). This rate is also supported by the increases in the annual kills of males from around 1924 to 1931 (Figure 1).

The dominant feature of the survival and reproductive rates as estimated for fur seals for a rate of increase of zero is that they are rather close to biologically reasonable or even logically possible maximum values. Thus, there is little scope for changes in these rates in a density-dependent response to changes in population size that would result in a rate of increase of 8%. To explore the implications of this limited range on the density-dependent mechanisms that are possible or reasonable for this population, we have calculated the percentage changes in each of several rates that would be necessary were an 8% rate of increase to prevail. We have considered the changes in each rate as a percent of the difference between the maximum value and the rate corresponding to a zero rate of increase for the population, as illustrated in Figure 7.

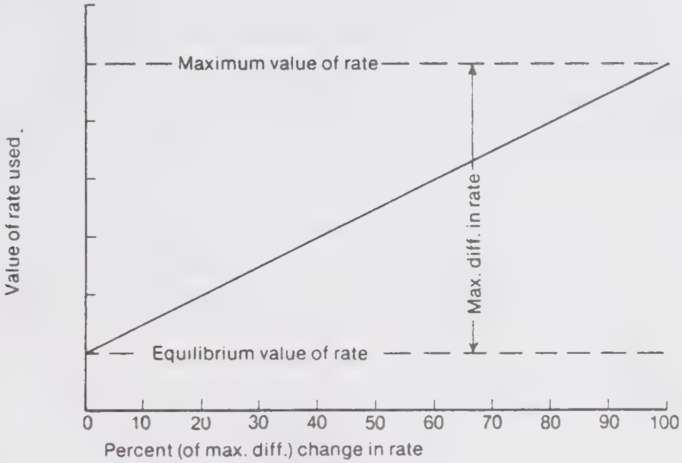

Figure 7 Diagram of the method of specifying changes in vital rates, as a percent of the difference between the biologically maximal value and the value at equilibrium. Values on the ordinate depend on the variable involved.

For survival the absolute maximum is obviously unity. We have little biological information to specify any values less than unity for this maximum. Estimated rates for ages 12 and 13 are around 0.94, suggesting that very high rates of survival are possible. Maximum values or survival rates may vary with age, as is observed for the estimated values. In particular, survival from birth through the first year probably has a lower maximum value than for any other age class, except perhaps for very old animals. Again, little information for a value below unity is available. However, it is not reasonable that the animals are capable of experiencing no natural mortality over any significant portion of their life span. In the present calculations maximum values in the range 0.96 to 1.0 were used for all ages above 3.

Maximum rates of survival from birth to age 3 are difficult to determine, as the animals are weaning, learning to feed in a new environment, and experiencing intensive growth during this period. Unlike pregnancy rates and adult survival rates, however, there is some information from the 1920s when the survival should have been higher if dependent on density. Chapman (1961, 1973) calculates the juvenile survival for this period as either approximately 31 or 36%, on the basis of estimates of the number of pups born, the number harvested from a year class (Table 5) and estimates of the possible number escaping kill. These values may represent maximal levels for this survival rate, but Chapman's calculations involve a number of assumptions that are not completely documented. We have further explored estimates of juvenile survival for this period with results which suggest that a rate of 54% may be a more reasonable upper bound (Smith and Polacheck, 1981).

Maximum values for reproductive rates are probably one pup per year for sexually mature females. Very little twinning has ever been observed (even in the period when the population was rapidly expanding). The sex ratio at birth is apparently even. This results in a maximum production of one-half daughter per sexually mature female per year. The proportion of the females that are sexually mature increases from age 3 up to age 6. The proportions may themselves be subject to changes as population size changes. For instance, it is observed that females collected in the western Pacific, primarily from Asian rookeries, show reproductive activity as much as one year earlier than those from the eastern Pacific. Thus for the younger ages the same maximum of one-half seems appropriate. The maximum reproductive rate for ages 1 and 2 is apparently zero as none have been observed to be sexually mature.

Using these maximum values for survival and reproductive rates, the life-table calculations suggest that if only reproductive rates are changed it is not possible to obtain a net rate of increase of 8% for any of the combinations rates considered in Table 6. The maximum rates of increase that can be obtained are at most a few percent. This is due to the estimated reproductive rates which are already high. The maximum rate of increase that can be obtained, for example, for the combination of rates labeled in Table 6 as "high" for survival rates and "central" for reproductive rates is 4.6 to 5.4%, depending on the value of survival from ages 3 to 4 used in determining the estimates for survival between age 3 and 12.

If only adult survival rates are changed, it is possible to obtain an 8% rate of increase for some of the combinations considered in Table 6. In particular, when the adult survival rates are low and when pregnancy rates are high, and given that the maximum survival rate possible is very close to 1.0, rates of increase of 8 to 10% are possible. It is necessary, in these cases, that the difference between the survival rates for a zero rate of increase and the maximum survival rates be large. This also requires that the pregnancy rates and the survival rates from birth to age 3 be high. Even so, the survival rates that are required to obtain 8% rates of increase are unreasonably high. Further, the percentage changes in adult survival rates that result in 8% rates of increase are on the order of 5 to 10%, changes that would be almost impossible to detect given the sampling variability apparent in Table 2.

If only juvenile survival rates are allowed to change, it is possible to obtain 8% rates of increase for many of the combinations in Table 6 with higher adult survival rates and pregnancy rates. These combinations result in smaller values of survival from birth to age 3 at equilibrium, and hence more range for possible changes in this rate. For example, for the combination of rates labeled "high" for survival rate and "central" for pregnancy rates in Table 6, the survival rate from birth to age 3 required to give an 8% rate of increase range from 61 to 79% for a corresponding range of survival from age 3 to 4 of 0.80 to 0.95. This range of three year rates correspond to unreasonably large annual rates of 85 to 93% if the rates were constant over the three years, and suggest that increases in juvenile survival of approximately 130% are required to obtain an 8% rate of increase of the population. Changes of this magnitude should have been relatively easy to detect, and are not suggested by the differences in the estimates of the survival rates in the 1920s and the 1960s, under any current interpretation of the data.

The general conclusion from considering the effect of changing one factor at a time is that the changes that must have occurred in the vital rates to account for the history of this population are not likely to involve only one of the three types of rates considered.

It is possible to consider changes in pairs of factors that could result in an 8% rate of increase. However, the number of possibilities and combinations becomes overwhelming quite quickly. Examination of some of these combinations gives an indication of the tradeoffs between changes in the different factors being considered can be obtained. Generally when two factors are being considered, only moderate changes in each are needed to obtain an 8% rate of increase. This is particularly worrisome, as the possibilities for detecting any such changes are related to the magnitudes of the changes. Thus as the numbers of factors changing increases, the possibilities for detecting the changes and hence determining which vital rates are involved, decrease.

DISCUSSION AND CONCLUSIONS

The Alaskan fur seal population has been considered as the one marine mammal population for which we have a good understanding of a population that has recovered from very reduced numbers while supporting a considerable harvest. In spite of this, the data and analyses presented here suggest that there are large gaps in our understanding of the dynamics of this population, both in the vital rates when the population was thought to have a rate of increase near zero and in the changes in the vital rates regulating the size of this population.

The major gaps in our understanding of the vital rates during a period of apparent zero population growth include estimates for the survival rates from ages 3 to 12, and for the survival rate from birth to age 3. While several analyses have been conducted to estimate values for some of these rates, such analyses are based on unsupported assumptions about several parameter values, and the sensitivities of the resulting estimates to these assumptions have generally not been considered.

Our analyses suggest that the survival of female seals from birth to age 3 must be substantially higher when the population is at equilibrium than the estimated lower bounds for this rate for juvenile males. Moreover, past estimates of survival rates for juvenile males (e.g., Chapman, 1961, 1964) when applied to females would require either or both adult survival and pregnancy rates near the upper range of the estimates presented in this chapter (e.g., Table 6) in order to be consistent with a net rate of increase that is nonnegative. This inconsistency between the estimates of the survival rates of juvenile males and the estimates of fecundity and survival rates of adult females has been reconciled in earlier papers by assuming that survival of juvenile females exceeds that of males by a constant factor (see Chapman, 1961, 1964, 1973).

However, given the lack of evidence for a differential rate of survival between males and females and the large uncertainties in all the estimated survival rates, there appears little reason to favor the assumption of differential rates of juvenile survival between the sexes in order to reconcile inconsistencies in estimates of the vital rates near equilibrium. Thus, within the ranges of the adult female survival and pregnancy rates presented here and what might be considered a reasonable range for estimates of the survival rate of juveniles near equilibrium based on estimates derived from the male kill, there are a large number of combinations of estimates that are consistent with a non-negative rate of growth without involving a differential survival rate.

The analyses of the changes in rates needed to obtain the observed high rates of increase in the 1920s indicate that there is not sufficient range in any one of the three major components of the life table (i.e., reproductive rates, survival rates from birth to age 3, and adult survival rates) for changes in one of these components to account for the observed dynamics of this population. These analyses strongly suggest that this population must be regulated by changes in at least two and possibly all three of these major components of its life table. If two or more of these components do vary with density, our calculations indicate that only small to moderate changes are needed in any single component to achieve a rate of growth of 8%. This fact may be responsible for the failure of the available data to provide convincing evidence for density-dependent changes and implies that an understanding of the mechanism regulating this population may be difficult to obtain.

While changes in more than a single major component of the life tables are biologically reasonable, the implications of this conclusion for managing this population are basically unexplored. The management for this population has been based on two concepts. The first concept, elaborated by Parker (1918), is that there are large numbers of male seals born that are not required to maintain the population. This has been shown to be true, at least in time frames of decades, as the populations continued to increase in the face of removal of large numbers of males. The second concept, introduced initially by Scheffer (1955), elaborated by Chapman (1961), and further developed (Chapman, 1964, 1973; Nagasaki, 1961; Bulgakova, 1971), is that changes in survival rates of young animals are responsible for the regulation of the population. The implication that the total yield from the population would be higher if both males and females were harvested has been drawn from this concept (Chapman, 1961, 1964). This deduction was tested by changing management policies from 1956 to 1966 to include a harvest of females. An increase in total yield did not result under this experimental harvesting regime. From the analysis put forward here it appears that this second concept on which management has been based, even if true, is insufficient in itself to account adequately for the dynamics of the population, and suggests the need to consider more complex models.

While our conclusions apply directly only to the Alaskan fur seal population breeding on the Pribilof Islands, the hypothesis that population regulation involves more than a single component of the life table should be considered for other large mammals which appear to have similar life tables at equilibrium with vital rates near their biological maximum (see Chapter 7). Mechanisms of regulation will likely be difficult to determine, since only small to moderate changes in vital rates may be occurring.

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ONE

An Overview of the Study of the Population Dynamics of Large Mammals

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HISTORICAL BACKGROUND

Verhulst's interest in human populations and the publication of his application of the logistic equation in the 1830s may be viewed as some of the original work in the formal study of the dynamics of populations of large mammals (see also Chapter 14). Most of the progress in this field, however, has been realized within the last few years. Over time, the character of studies involving large mammal populations has changed as have studies on animal populations in general. Early investigations focused primarily on the capacity of populations to increase. The study of factors involved in preventing unlimited growth acquired more importance later. These same trends characterize the study of population dynamics at other taxonomic levels with an apparent tendency for studies of large mammal populations to lag behind studies of other groups. An excellent discussion of the general history of the study of populations can be found in Hutchinson (1978).

From a taxonomic perspective, the study of population dynamics has shown a tendency to focus on humans, microorganisms, insects, fish, birds, and, to some extent, on small mammals. Comparatively little of the effort expended in the field of population dynamics has involved large mammals other than humans. There are several factors that, in combination, have contributed to this discrepancy. Although often of importance to man, undomesticated large mammals in general are neither as influential as pests nor as important as food sources as are many smaller organisms. The study of the natural history and general biology of large mammals is easier than, and has often precluded or taken precedence over, the study of their population dynamics. The long-lived nature of large mammals (see Chapters 2, 22) prevents the rapid accumulation of data that is possible with populations of small organisms, especially those that can be reared in the laboratory. Obviously, there are fewer species of large mammals than of the smaller-bodied species. Together these factors seem to be the basic cause of a rather short and relatively unproductive history of the study of population dynamics of large mammals.

Most studies involving population dynamics within all taxonomic groups have involved either species of economic interest or man's own population. This has encouraged a narrow perspective oriented toward solving specific problems or achieving specific goals. By comparison, a philosophically more general or academic view of population dynamics has evolved through studies of birds, microorganisms reared in laboratories, and other groups of species that are relatively less important to man.

This trend is especially obvious among studies involving large mammals. As we will discuss them, most studies of the dynamics of large mammals involve three groups: (1) humans; (2) large terrestrial mammals (as predators, tourist attractions, or game animals); and (3) marine mammals (being larger and of economic value). In all cases, most studies involve species of direct importance to man. Few studies of the population dynamics of large mammals are conducted out of pure academic interest. Some of the studies on the George Reserve deer herd (McCullough, 1979), for example, provide a notable and very valuable exception.

The study of the dynamics of human populations has an interesting history. Having started with a conceptually holistic approach embodied in the logistic equation, the work on humans has become deeply engrossed in the effects of structure by age, sex, and reproductive potential, migration, socioeconomics, and other dimensions of importance to short-term projections. The concept of an upper limit to the population (or carrying capacity) has been of much less importance than would have been predicted on the basis of Verhulst's first consideration. Today the bulk of the theory involving dynamics in age-structured populations is to be found under the authorship of people who have worked with human populations.

Increasing impact, brought about by man's growing population and growing interest and concern by the public for the protection of certain species, has created new demands for a better understanding of the ways in which large mammal populations change over time. In terrestrial environments man has long had an interest in protecting, harvesting, or controlling the populations of specific species of large mammals. As in the case of studies involving humans, the study of these species has often progressed to a level of resolution that has, to a degree, prevented the development of holistic views. Studies in these situations have often emphasized minute details of the relationships between the animals and their environments, especially their resources. These studies have generally been less quantitatively oriented than have population studies of humans, insects, and fish. Most studies of terrestrial large mammals have thus resulted in a fairly detailed understanding of the natural history of the species involved. As a result we often know more about the husbandry of these species than we do about either how the populations are regulated or patterns in their dynamics. Specific needs for management and for short-term predictions have worked against the development of a holistic understanding of the population dynamics of large mammals.

Nonetheless, the general need for a holistic view of population regulation is growing in importance as increasing numbers of species of terrestrial large mammals are being managed within the context of their ecosystem. There is a growing need for a general perspective within which such management and future research may be conducted if management is to be realistically based on ecosystem principles.

The mathematical modeling of terrestrial populations of wild large mammals has been attempted only in recent years. Much of the delay in such activities has been a product of insufficient training (see Chapter 21). Most people who have worked with populations of large terrestrial mammals have not been given the mathematical background that is more characteristic of those studying fisheries, human populations, or marine mammals. Those who have attempted to undertake quantitative studies have tried to use life tables without realizing that such an approach is less of a dynamic model than a static description. This weakness is being avoided more in recent work as age-structured matrix models and other more elaborate but less analytically tractable models are being used with the help of computers. Many chapters in this volume exemplify the progress currently being made.

Many large mammals in marine environments are of economic value. The history of the harvest of these species is long and, in some cases, relatively well documented. Technological advances in harvesting techniques have resulted in the extinction, or near extinction, of a number of species. Compared with our view of the population dynamics of terrestrial species, we have a more holistic view of the dynamics of marine mammal populations. This situation has been forced on us by the nature of their environment; detailed examinations of the relationships between marine animals and their environment is prohibitively difficult. Most of the information useful for studying the population dynamics of marine mammals has come from harvest records. As in the case of fish, these data are collected in terms of numbers, ages, pregnancy rates, and weights. The dynamics of each of these attributes of harvested populations has been scrutinized in relationship to the other attributes without the benefit of a detailed understanding of their behavior, physiology, and interaction with other species.

It was not until the 1960s that quantitative syntheses of the data for marine mammals began to take the shape of population models (e.g., Chapman, et al., 1964). The studies that were of greatest importance involved the effects of harvest on exploited populations. Unfortunately, many of these studies were based on previous studies of fish and, to some extent, insect populations. The study of fish was also characterized by data involving numbers, weight, and age, as indicated by the catch. This similarity in data led to a natural tendency to borrow models from older work on fisheries to be applied to marine mammals. As is the case for terrestrial populations, much of the current work on marine mammals is beginning to take on its own identity, overcoming the sometimes inappropriate approaches inherited from early studies in the field of fisheries.

GENERAL APPROACH

Most approaches taken in the study of populations take one of three basic forms. The first is the approach taken by natural historians. This is least formal and is basically descriptive. Little if any attention is paid to the utility of any paradigm developed. The intuitively appealing, intriguing, and visually apparent aspects of a given species' population biology are emphasized. The second approach involves conceptual models formalized in written narrative. This makes a conscious recognition of the existence of the animals in the context of a population. The third approach uses formal mathematical models to describe these populations. Although parts of a continuous and complementary spectrum, these overlapping categories of approaches are useful for discussing the field of population dynamics. It is the more formal approach that we attempt to emphasize through the chapters that make up this volume. Our bias is toward this type of study and, when overwise left unspecified, we will be referring to this approach with the term "population dynamics."

Studies of terrestrial large mammals have often been primarily a process of developing a description of their natural history. Partly because of the length of time required for sufficient data to accumulate, only recently have more holistic, formal treatments of the population dynamics of terrestrial large mammals been developed. An examination of the chapters in this volume, the literature cited herein, and a bibliography of population dynamics in large mammals (Fowler et al., 1980a) illustrates that relatively few organized or specialized efforts have been made along such formal avenues. In many cases, however, there exist relatively unutilized data sufficient for studies involving the production of a formal synthesis. Many populations in Europe, Asia, and North America have been monitored for years. An important need is to identify such sets of data and to utilize this information in formal syntheses to improve our understanding of the dynamics of terrestrial large mammal populations.

Compared with that of terrestrial large mammals, our knowledge of the natural history of marine mammals is limited. Basic biological data often have come solely from animals captured in the harvest, rather than from observations of animals in their natural environment. Motivated by international as well as national concerns, various studies focusing primarily on the dynamics of marine mammal populations were first seriously approached during the 1960s when several formal mathematical models were first applied. The pioneering work of D. G. Chapman on the northern fur seal (Chapman, 1961, 1964, 1973) and with others on the great whales (Chapman et al., 1964; and subsequent volumes of the Reports of the International Whaling Commission) was important in this regard. As mentioned earlier, these studies drew heavily on techniques and concepts developed in earlier studies of fish populations. As will be amplified later, the governments sponsoring such research needed relatively precise evaluations of the size and rate of production of the populations in question in order to provide specific advice for management.

For both terrestrial and marine large mammals, there is a growing need to refine the underlying conceptual models. In most instances, this means that the basic biology or natural history of the species involved should be better utilized in the construction of these models. For terrestrial species this involves using the existing information to extract general principles, while for marine populations this involves the need for more such information. By virtue of this contrast we encounter one of the basic differences in studies of large mammals in these two environments—the difference in resolution—an attribute discussed in the next section.

The study of the dynamics of human populations has developed very differently from the study of the population dynamics of marine and terrestrial large mammals. Studies of human populations involve very formal mathematical models, the third approach discussed above. These models are firmly grounded with precise and detailed descriptions of vital rates, almost always on an age-specific basis. But the underlying conceptual models do not appear to be self-contained. For example, the fact that vital rates (birth, mortality, and so forth) do change is accounted for, but as external input rather than as changes that can be accounted for within the models. (See Chapters 15 and 19 for work of this type on animals other than humans.)

A great deal of attention in the models used in the study of human populations is given to structure, distribution, and details of importance in short-term predictions. Precision over short time spans is more important than are long-term changes, trends or patterns. Very little emphasis is placed on factors of ultimate importance in establishing an upper limit to the human population. Feedback by way of density dependence is rarely if ever included. In comparison to the classic models of marine mammal populations, the models of human populations are quite resolute. In contrast to most models of terrestrial large mammals, and many for marine mammals, models of human populations involve a great deal of internal dynamics relating to age and sex structure.

Because of technological support behind the growth of human populations, relatively little evidence has been found for the existence of density dependence (see Fowler, 1981, Chapter 23). This has led to the abandonment of the logistic that was one of the earliest models to be applied to populations of large mammals (Pollard, 1973). By contrast, considerable evidence for density dependence in large mammals (Fowler et al., 1980b, Chapter 23) exists. Most of the formal models of large mammal population dynamics for nonhuman species involve density dependence as seen in many of the chapters in this book.

As a result of research involving human populations and the supporting theory, we have a very detailed understanding of the process of population growth as it relates to such factors as age structure, reproductive schedules (reproductive value by age), age at first birth, and life span. This is an example of study that has taken a very resolute formal quantitative approach to specific aspects of population dynamics. It is to be contrasted to attempts to incorporate a great deal of resolution into our representations of the interactions between populations and their environments, a matter of scope as discussed in the next section. Such approaches include a larger system, but often with less detail or resolution involving the population itself.

SCOPE AND RESOLUTION

Among the most important aspects of the design of studies of large mammal populations are those of scope and resolution. The breadth of a study and the degree of detail involved are determined by the questions to be addressed. Several dimensions of scope and resolution as involved in studies of large mammal populations are addressed here.

It is important to point out that separate studies of the same population, with different scope and resolution, can be mutually complementary to our understanding of the dynamics of that population. Studies of marine mammals, of terrestrial mammals, and of humans, however, have each tended historically to retain separate sets of goals that are different among, and consistent within, groups. Too frequently this has led to marine mammals being studied nearly consistently at one level of resolution, and humans, for example, at an entirely different level. In view of the fact that studies at different levels of scope and resolution are complementary, it would seem useful to design two studies of an elephant population, for example—one to answer questions generally asked about whales, and a second to answer questions generally asked about humans. Such complementary studies, applied on a large scale, would enhance our overall understanding of the dynamics of large mammal populations.

In all cases the design of studies of populations of large mammals must deal with the overriding problem of resolution, or the degree to which detail is involved. The proper resolution of any particular study is determined by the questions being addressed. The realizable resolution is determined by the existing data, logistical constraints, time, and money. Practical considerations or management-oriented questions often demand precision and predictability at the expense of generality. General principles that often emerge from questions that are more academic in nature, and that demand more generality in approach, are often sacrificed.

Of similar importance is the scope of factors thought to be influential in determining the nature of the dynamics of populations. Can a population be represented adequately by a model involving only the population's numbers and its essential internal characteristics alone? Or do we need to include other elements, such as those of the ecosystem, to capture the essential features of the dynamics of interest. As with the resolution of a model, the scope of a model must be determined largely by the questions being addressed. However, a growing body of theoretical and empirical background would indicate that the proper scope of such studies depends in part on the species involved. Small-bodied "r-selected" species seem to be more at the mercy of their environment than are large "K-selected" species, and hence may require more scope in the models developed to represent them.

Even so, greater scope may be required in meeting the objective of much of the current work on large mammals. In managing the harvest of the great whales and the Alaska fur seals, for example, it has become increasingly clear that the degree of interspecific interactions, both among harvested species and between the harvested populations and their food sources, is considerable (see Chapters 2, 14, 17). It has been estimated that southern hemisphere sei whales may have increased by more than 60% in population size owing to changes in their reproductive rates prior to their being exploited (Smith, 1977; but see also Mizroch, 1980). Similarly, a major area of research is the possible effect of changes in fish populations in the Bering Sea, due to increased fishing effort, on fur seal population size. In both cases the traditional models of limited scope, in providing advice for management, cannot be realistic in accounting for these interactions; but these models can and do provide advice that is precise (discussed below).

Such considerations do not negate, however, the utility of single species models for many purposes. A production model (such as the generalized production model discussed in Chapman, 1960; Richards, 1959; Pella and Tomlinson, 1969) with stochastic properties may capture the essential elements of the dynamics of a broad spectrum of species. Greater degrees of stochasticity (more variance) may be needed for those species that are more subject to their physical and biological environment. The interaction of the species with its biological environment (the ecosystem aspect) may, in large part, be captured by the parameters of such models (e.g., see Fowler, 1980a, 1981).

Obviously, permanent or unusual changes in the ecosystem are not going to be reflected in simple models (see Chapter 17). In addition, it may facilitate our understanding of the ways in which simple models should be parameterized to conduct studies in which a greater scope is included. Thus the more complex ecosystem models are of obvious value, and work along these lines should be encouraged. Progress along these lines will, by necessity, be slow, however, because the quantity of information required often proves prohibitive. (See Fowler et al., 1980b; Chapter 14.)

PRECISION, REALITY, AND GENERALITY

Levins (1966) identified three features of models constructed to represent natural systems. These were generality, precision, and realism. He points out the difficulty (if not impossibility) of obtaining strength in all three of these attributes in one model. One or more must be sacrificed to obtain a strong representation of the others. Different tradeoffs have strength and utility in particular applications. In the study of population dynamics, these principles can be used in evaluating and comparing the various approaches being taken.

Some of the chapters in this book argue that more reality should be included in models of the population dynamics of large mammals, through an increase in scope, especially in terms of the interaction of populations with their environment (Chapters 2, 15-19, 23). It is argued that simple models, such as the logistic, although they implicitly reflect interactions with environments, are often not sufficiently realistic. Some generality and realism are sacrified despite the fact that such models capture several basic concepts of importance. Botkin et al. (Chapter 19) present examples of how specific types of information concerning factors external to populations can potentially affect our views of the ways they behave. Both Caughley (Chapter 18) and Fowler (Chapter 23) argue that interactions between trophic levels may produce overriding effects on the types of dynamics to be expected. These latter arguments attempt to achieve some degree of generality and realism by sacrificing precision. Horwood's chapter (Chapter 17) deals with other interactions between species, sacrificing precision and some generality in an attempt to be realistic. Generality is of less importance than either precision or reality in McCullough's work on grizzly bears (Chapter 9). Somewhat of a balance seems to have been struck by the model behind the chapter by Pojar (Chapter 12), in which only a limited proportion of all three features is achieved.

As argued earlier, one way of dealing with the impossibility of producing a complete representation of reality in one model is to produce several models of the same system. As Walters et al. (Chapter 16) have described, several models of different levels of resolution (and hence precision, reality, or generality) may be produced for examining questions from different points of view. Frequently not well recognized is the possibility of constructing several different models of the same system, instead of developing one in great detail. Although difficult to implement, such an approach emphasizes the problems created by the fact that no model is perfect. Relying on one imperfect model regardless of its resolution can create serious problems.

An interesting example of the balance among realism, precision, and generality appears in the population studies developed to provide advice for the management of several groups of marine mammals. The constraint of providing specific defensible advice to regulatory bodies such as the International Whaling Commission, the United States National Marine Fisheries Service, and the North Pacific Fur Seal Commission has prompted models that emphasize realism and precision — especially the latter — at the expense of generality.

Studies by Chapman and others referenced above for the International Whaling Commission were designed to provide advice to the political decision-making body. The results of these studies had increasing impact on the actual decisions about quota levels that were made through the 1960s and into the 1970s. For different points of view on this, see McHugh (1974), McVay (1974), and Smith (1976). In order to be useful in a sometimes adversarial context, it was necessary that the advice given be quite specific, requiring very high precision in the models being used. It was generally more important that estimates of the effect of various harvest levels be precise than that they be obtained using realistic models. Certainly both of these aspects far outweigh the need for generality in this context.

Very likely, in the interest of providing advice in a usable fashion, the precision of the results of studies on the population dynamics of the great whales has, from time to time, been oversold (Smith, 1976). Certainly decisions have been made primarily on the basis of point estimates, rather than on statistically more meaningful interval estimates. Indeed, in some instances simple sensitivity analyses of the models being used have only recently been undertaken.

Another result of this emphasis on precision is that the scope of the models developed within the context of management has remained quite narrow. They are almost always single-species descriptions, and are heavily dependent on the concepts of density dependence, carrying capacity, and maximum sustainable yield. In fact, the emphasis on precision has, at times, resulted in these concepts being built into the legal framework (national and international) that provides the context in which management decisions are made. Thus the stated management objective for the northern fur seal is maximum sustainable yield. Similarly, the much more general concept of optimum sustainable population level (OSPL), as used in the U.S. Marine Mammal Protection Act (MMPA, Public Law 92-522, 1972), has been interpreted for purposes of managing the incidental kill of porpoises by tuna fishermen as a population size between the level giving maximum sustained yield and the carrying capacity (Smith, 1979).

The problems of management in the context of not being able to provide relatively precise advice are very great. When it becomes apparent or likely that the models being used are rather more precise than they are realistic, or accurate, what is to be done? In the case of the great whales the information available is insufficient to allow creation of new models of greater realism without greatly sacrificing precision. Yet without the level of precision that management decisions have come to depend on, these decisions are more likely to be based on political and economic pressures, too often to the detriment of the long-term productivity and viability of the populations.

Studies of the populations of porpoise in the eastern tropical Pacific illustrate this point in directly acknowledging the problems of realism. Animals of these populations are known to associate closely with schools of yellowfin tuna. Fishermen using purse seines utilize the surface-swimming porpoise as indicators of the presence of tuna, resulting in the incidental killing of some porpoise. Management decisions about allowable incidental kill levels are based, in part, on fairly precise, but rather simple, population models (Smith, 1979; Smith and Polalcheck, 1978). Because of the apparent symbiotic relationship between the tuna and some populations of porpoise, the co-occurrence of several species of porpoise and of tuna, and the reduction in abundance of both the porpoise and the tuna populations, it is reasonable to expect some interspecific relationships to be important. Current management actions are based on a model that is precise, but more general than realistic.

This single-species model was selected as the best for generating management advice when it was realized how difficult it would be to deal with the interspecific interactions. It was *not* decided that a less precise but more realistic multispecies or ecosystem model would be appropriate for management advice. The loss in precision to gain this realism would have been so great as to preclude any utility of the management advice that would be produced. Interestingly, in court challenges to the management decisions that have been made on this advice, the adequacy of the scientific advice is being attacked not in terms of the realism of the models, but rather in terms of the precision of specific parameter estimates used. Thus the decision that precision could not be sacrificed to gain realism is probably reasonable from the perspective of management. Frequently this emphasis on precision over realism has been shown to be a necessity if rational management decisions in adversarial context are to prevail. Indeed, without reliance on such concepts as carrying capacity and maximum sustained yield, the management of marine mammal populations would be governed far more by short-term economic interest than by interests concerning long-term renewability.

COMPARATIVE APPROACHES

Another way of gaining insights into the nature of any specific population and its dynamics is to view it as an example of particular types of populations, and on the basis of the properties of each of the larger groups to deduce the properties of the particular case. This approach presupposes that groupings of populations can be described on the basis of samples of populations drawn from that group. Comparison of the dynamics of populations of various categories should lead, in theory, to general principles of use in deducing properties of specific populations.

It is the apparent lack of attempts to make comparisons and to formulate generalizations concerning the nature of the population dynamics of large mammals that provided the general stimulus for convening the conference at which the contributions to this volume were originally presented. In this volume the chapters by Bunnell and Tait (Chapter 4), Chapman (Chapter 14), Goodman (Chapter 22), and Fowler (Chapter 23) (as well as the unpublished papers by Holt and Beddington presented at the conference) deal with this issue directly. Others treat the issue less directly. As more papers of similar nature are produced, the potential for such approaches will become more apparent. The work of Harestad and Bunnell (1979) and Smith (1974) falls into this category along with work recently completed by Fowler (1980a, 1981). The principles having their origin in such studies can help provide a perspective within which each special case may be considered. Such studies must rely, however, on a general background of information contained in papers similar to those in this volume and in the general literature. It is hoped that this book will be of help in stimulating further work along such lines.

In attempting to generate comparisons, schemes must be formulated that result in classifications across which comparisons can be made. Examples can be produced on the basis of the chapters in this book. One of our first objectives was to provide a sampling of marine and terrestrial work that could be used for initial contrasts and comparison in the format of the conference and this book. It was hoped that consideration of what is known in terrestrial settings could be of material help in gaining a better understanding of the dynamics of the marine species, and vice versa. As noted earlier, one difference seen in comparing these two groups of papers is that the terrestrial species are represented by studies with greater resolution than are the marine species. A further difference to be kept in mind is that the major problem facing many species of marine mammals is the danger of their being overharvested. They are less likely to be subject to habitat destruction, a problem common to many terrestrial species.

It is difficult to determine which comparisons will result in the greatest progress in our understanding. There are, however, a number of dimensions across which theoretical and empirical comparisons could be made to help develop our view of the population dynamics of large mammals in particular and of animals in general. In addition to longevity, initial survival, age at first reproduction, birth, and mortality, as discussed by Fowler in Chapter 23, there are such factors as social organization, territoriality, and taxonomic categories. The 12 characteristics mentioned by Eberhardt and Siniff (1977) as potentially useful for evaluating a population may serve as bases for comparison as well. Some of the attributes mentioned above are part of the "life-history strategy" that must serve as a basis for comparison as discussed by Goodman (Chapter 21) and Fowler (1981). Various categories of specialization and behavioral types may serve as fruitful categories for comparison. Growth rates and specific productivity are further dimensions for potential comparisons.

There are numerous studies on species of terrestrial herbivores (such as the ungulates in general). There is relatively less work that deals with terrestrial carnivores, but progress is being made (see, e.g., Chapters 6 and 16). As emphasized in the chapters by Fowler (Chapter 23) and Caughley (Chapter 18), the dimension of trophic level may be an important dimension across which to make comparisons. Specific arguments for expecting differences between trophic levels were developed by May (1973), Fowler (1980a, 1980b), and May et al. (1979).

Numerous types of comparisons can be made across the dimensions identified above. As discussed in Fowler (1980a; Chapter 23), the shape of productivity curves can be compared. These are of special interest in management and from the point of view of the roles played by the populations in their respective ecosystems. Comparison may be made between such attributes, since they may be correlated. There may be a tendency for populations of large-bodied species to exhibit regulation through change in birthrate, as opposed to change in juvenile survival, which may be of more importance in the regulation of smaller-bodied species. Such correlations, if they exist, can only be recognized through comparison. As shown by Harestad and Bunnell (1979), there are relationships between the size of territories (range) and body size, trophic status, and resource productivity.

There are a number of specific questions and hypotheses that need to be addressed as they relate to matters of practical importance. In particular, the scientific committee of the International Whaling Commission is in desperate need of insights useful in developing more realistic approaches to setting quotas or deciding which stocks should receive protection. As carnivorous large-bodied and socially organized large mammals, do cetaceans exhibit dynamics that can be described on the basis of what we know about large-bodied species combined with what we know about the socially organized species and carnivores in general? Do social groups of cetaceans exhibit territoriality in ways in which our growing knowledge of the effects of territoriality in terrestrial systems may be applied? Are there genetically determined differences between the various taxa, or are population dynamics more a product of the nature of a species as independent of its taxonomic relationship to other groups?

Before leaving the topic of comparative population dynamics, it should be noted that we do not wish to underemphasize the need to make comparisons across a much wider spectrum of species types than is encompassed by large mammals alone. The study of large mammals in particular and animals (and possibly plants) in general should profit from broad comparisons. As pointed out by Fowler (1980a, 1981), patterns concerning population dynamics seem to be emerging as a result of comparisons made across the spectrum of body size, *r-K* strategies, longevity, and productivity. These comparisons need both theoretical and empirical underpinnings to provide the progress we need toward a better understanding of the population we wish to manage. Through such studies we may better appreciate the errors made in adapting models developed in the study of fish and insects to the study of large mammals.

THE SCOPE OF THIS BOOK

The chapters included in this book are examples of studies of large mammals that provide a basis for comparisons of two types. First, each chapter contains information concerning individual species such that species may be compared as outlined in the previous section and as discussed in Chapter 23. Second, the studies themselves can also be compared, as outlined in earlier sections. Such comparisons are a necessary part of coming to grips with a truly comparative study of population dynamics. The basis for comparisons in each case is not always well defined; indeed, it is the principal problem of comparative science to explore the possible bases, searching for those from which new insights can be obtained.

Some sample bases for comparison of both types are shown in Table 1. In this table the columns are grouped into six categories. The first two categories represent material for comparisons over the characteristics of the species involved. The remainder represent comparisons that may be drawn between and among the studies themselves. In all cases Table 1 contains an indication of how each chapter has been categorized, to show the scope included in this book. In addition to the bases for comparison outlined above we have indicated the continent of origin of the senior author of each chapter.

The absence of chapters dealing with studies of human populations (see columns labeled *Group of Mammals*, Table 1) is regrettable. Although two contributions were planned, conflicts in schedules resulted in cancelations. This lack is unfortunate, as much of the theory of population growth has been developed within the context of research involving humans (see, e.g., Pollard, 1973; Keyfitz, 1968). The work on humans, however, has taken on a very different character from studies of other large mammals as discussed above. Inter-

Table 1 Classification of Chapters in This Volume Across Several Dimensions

First Author	Chapter	Group of Mammals			Trophic Level			Approach			Scope			Levins's Categories			Continent					
		Terrestrial	Marine	Human	Herbivores	Carnivores	Omnivores	Descriptive	Conceptual	Formal	Single Species	Multispecies	Ecosystem	Realism	Precision	Generality	Africa	Europe	Australia	N. America	S. America	Asia
Allen	13		x			x			x	x	x				x	x			x			
Botkin	19	x			x				x	x			x	x		x				x		
Bunnell	4	x				x	x	x	x			x		x		x				x		
Burgoyne	21	x			x				x	x	x			x		x				x		
Caughley	18	x			x			x	x			x		x		x			x			
Chapman	14		x			x			x	x	x				x	x				x		
Croze	15	x			x				x	x		x		x		x	x					
DeMaster	20		x			x			x	x	x			x		x				x		
Eberhardt	10		x			x			x	x	x			x	x					x		
Fowler	23	x	x		x	x	x		x	x	x	x		x		x				x		
Goodman	22	x	x		x	x	x		x	x	x			x		x				x		
Hanks	3	x			x			x	x			x					x					
Harris	11	x			x				x			x		x		x				x		
Harwood	8		x			x			x	x	x			x	x			x				
Horwood	17		x			x			x	x			x	x		x		x				
Laws	2	x	x		x	x		x	x			x						x				
Lett	7		x			x			x	x	x				x	x				x		
McCullough	9	x				x	x	x	x	x	x			x	x					x		
Pojar	12	x			x				x			x		x		x				x		
Smith	5		x			x			x	x	x			x	x					x		
Starfield	6	x				x			x	x	x			x	x		x					
Walters	16	x			x	x			x	x		x		x		x				x		

action between students of human populations and students of other large mammal populations is needed, as humans are large mammals.

The collection of chapters in this book may be distributed along a spectrum ranging from single species to ecosystems. As mentioned earlier, the single-species approach makes the assumption that the essential dynamics of a population can be characterized as abstracted from its environment. The ecosystem approach carries the philosophy that the ecosystem may provide the overriding driving forces that determine the dynamics of any particular species. As shown in the columns labeled *Scope* in Table 1, there is preponderance of chapters that take the single-species approach. This partly expresses our bias toward working along these lines as well as the fact that most work is being conducted at this level. The latter should be viewed as a gap in the approaches being taken, and the recommendations being given by Botkin et al. (Chapter 19), Croze et al. (Chapter 15), Caughley (Chapter 18), and others in this volume should be taken seriously. Ecosystem models and results of research conducted at this level should be examined for a better understanding of the cause-and-effect relationships contributing to particular types of dynamics. Simple, general, single-species models should be examined for the differences and similarities that exist between various groups or types of populations as categorized on the basis of their interactions with their ecosystems.

There is a relatively large number of species of terrestrial herbivores in comparison to carnivores. In spite of this differential, this book contains a number of chapters that deal with carnivores (see columns labeled *Tropic Level*, Table 1). McCullough's chapter on bears (potentially classified as omnivores, Chapter 9), the chapter by Starfield et al. on lions (Chapter 6), and the treatment by Walters et al. on wolves (Chapter 16) exemplify advances being made in our understanding of the population dynamics of these higher trophic levels. It is apparent that interactions *within* the populations of such species is of great importance. It is important to know to what degree these interactions override those with other elements of their ecosystem.

Three levels of approaches to the study of populations were identified above: descriptive, conceptual, and formal. The chapters in this book are categorized in these terms in Table 1 under the column labeled *Approach*. Most include aspects in two of these three categories, and all include some level of conceptual modeling. All the chapters, of course, rely on descriptive studies at some point, even if this is not specifically discussed.

Levins's (1966) three attributes of realism, precision, and generality discussed above provide another basis for comparison of the chapters in this volume. Our categorization of the studies presented in this volume as they achieved a balance among these aspects are indicated in Table 1 in the column labeled *Levins's Categories*. Although classifying chapters into these categories is a matter of judgment, it appears that most of the contributions favor realism and generality at the expense of precision. Somewhat fewer favor realism and precision, while fewest favor precision and generality. These relationships are different for studies on terrestrial and marine mammals.

In trying to obtain a diverse sampling of workers and populations we attempted to attract to the conference a number of individuals from countries other than the United States. As shown in the columns labeled *Continent* in Table 1, we succeeded in obtaining three contributions from Africa, two from Australia, and three from Europe (plus two not published). Financial constraints and a large population of workers in the United States resulted in an imbalance, wherein almost one-half the participants represent North America.

It should be noted that a great deal of work has been conducted by the Japanese. In particular, there has been a considerable effort spent in dealing with marine mammals, especially fur seals as well as both large and small cetaceans. The Soviets have conducted some work along these lines, and considerable data exist among the western Asian and European countries concerning several terrestrial species. There seems to be an opportunity for progress in these areas.

DIRECTIONS FOR THE FUTURE

We have tried to present a general description of our view of the history and perspective of studies involving the population dynamics of large mammals and to place this book within that perspective. In presenting the history we have tried to point out the important differences between approaches taken by various disciplines within the general field. The strengths of each approach may be used to aid progress in the others. We have provided a general perspective with the view that each type of model has its own merits. Specific questions require specific avenues of research. We have discussed general comparisons and emphasized this aspect of the study of the population dynamics of large mammals because, in the past, little attention has been paid to academic issues, general principles, and overall perspective.

To promote the progress that seems possible, several things are required. The first is a need to standardize the definitions and concepts behind terms being used within the field of population dynamics, especially as they are used by biologists studying large mammals. The term "carrying capacity" is a good example. Most theoretical population biologists and population dynamicists working in the fields of fisheries and entomology use the term to refer to that mean population level that would be observed under conditions unaltered by man. It is often referred to as the constant K in the deterministic logistic equation. Range specialists, however, as investigators who deal with many species of terrestrial ungulates, define carrying capacity in terms of the conditions of the forage. Such differences must be resolved before any meaningful communication between disciplines can take place.

Second, the specialists working in the field of population dynamics of large mammals need to recognize the existence of other work both within their specific field as well as in the general field of population dynamics. As mentioned earlier, there is a need to identify existing sets of historical data and to subject them to formal analysis to help overcome the problems created by the long-lived nature of large mammals. A specialized course in this field at several major universities would prove fruitful and could draw on the resources now available in the published literature. Symposia and conferences such as that which resulted in this book are to be encouraged. One or two specialized centers for research in this field would help provide coherency. The publication of a journal specializing in the population dynamics of large mammals would be of considerable help. The field has an identity and integrity of its own, and recognition of the existence of the collections of published papers, data, and workers doing this type of work will help promote the progress needed.

Hand in hand with recognizing and being familiar with the breadth of work in other aspects of the field of population dynamics in its application to large mammals is the need to undertake complementary studies, as mentioned earlier. Work on any single population or species can be made much more productive by taking separate approaches with different scope, resolution, levels of formalism, realism, precision, and generality. Since most of these attributes are determined by practical considerations, there is a need to emphasize academic studies—studies presenting more general and less restricted questions and hypotheses. Broader interest in conducting such studies should be encouraged.

There is clearly a great need for catalyzing and supporting further work on the population dynamics of large mammals. As man's population continues to rise, we encounter increasing numbers of problems that involve the populations of other large mammals. Many species such as the elephant and bison are restricted to ranges much smaller than previously occupied. In many cases these ranges continue to decrease because of habitat destruction. Other populations are either depleted or are overharvested. There are conflicts involving other resources, such as exemplified in the cases of tuna, porpoise, and gray seals (see Chapters 8 and 17). Predator control and its direct and indirect effects continues to be of concern. Growing public concern over sound management or complete protection places us in a particularly good position for requiring more understanding of the effects of various alternatives. More thought is needed regarding future options in place of current demand. One of the purposes of this chapter and of the book as a whole is to provide new insights of value in making this progress, to underline the need for continued effort, and to help provide some alternatives for fruitful study.

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Profiling Pelagic Fish Schools Using Airborne Optical Lasers and Other Remote Sensing Techniques

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INTRODUCTION

There is an increasing interest among researchers involved in fishery exploration and stock assessment in the use of airborne techniques to assist in the assessment of pelagic fish stocks. Of particular interest is the development of airborne remote sensing techniques to scan and locate fish schools or school groups, and to examine individual school size in both the vertical and horizontal plane. Rapid real-time assessment of fish stocks is necessary for the management of coastal pelagic schooling species that have a relatively short life span. Real-time data are needed for the management of common pelagic species off the west coast of the United States such as northern anchovy *(Engraulis mordax)*, Pacific bonito *(Särda chiliensis)*, Pacific mackerel *(Scomber japonicus)*, and jack mackerel *(Trachurus symmetricus)*.

Visual detection by commercial aerial fish spotters is one form of remote sensing which has been used for many years to detect fish schools or school groups in both daylight and nighttime conditions; a number of commercial fisheries use this technique to increase the catch of fish (Squire, 1961, 1972). During daylight hours the human eye can detect color, shape of school, and movement of fish within the school as keys to species identification. Visual sightings at night rely on the observation of bioluminescence generated by planktonic organisms as they are disturbed by individual fish within a school. On many occasions differences in the behavior patterns of the various species, resulting in different bioluminescent patterns, make identification more positive at night than during the day. Photographic techniques have also proved valuable in the measurement of fish schools.

These techniques for remote fish detection have limitations. Visual or photographic detection of fish schools during the day relies upon the fish school being relatively near the ocean's surface as illumination, sea state and turbidity can limit visibility. At night, viewing the bioluminescent pattern of a fish school is possible only during periods of very low illumination levels from the moon, or periods of no moon. The bioluminescent characteristics of the phytoplankton and its concentration are also limiting factors.

Airborne electronic remote sensing viewing devices such as low-light level video systems (LLTV) also have many of the same limitations as visual observations. However, the limitation of flight at the low altitudes necessary to visually detect bioluminescent targets is eliminated with the advanced LLTV systems, and this allows scanning a large geographic area from altitudes of 1,300 to 2,000 meters (3,900 to 6,100 ft). Surveys can sometimes be conducted during periods of low level reflected illumination from the moon or shoreline sources, thereby increasing potential survey time.

Airborne remote sensing for fisheries has used image intensifiers and LLTV systems. Some of these are fixed vertical view systems using commercially available electronics (Roithmayr, 1970; Cram, 1974); others are highly specialized LLTV scanning units with electronics specifically designed for viewing targets in the bioluminescent spectral wavelength (470-480 nm). The LLTV system developed specifically for fishery surveys by Zapata Fisheries Development Corporation has been used to evaluate the stocks of anchovy off northwestern Mexico (Figure 1), sardine and mackerel off Chile and Southwest Africa, tuna off Central America and tuna, herring, thread herring and menhaden off the U.S. Atlantic and Gulf of Mexico coastlines.

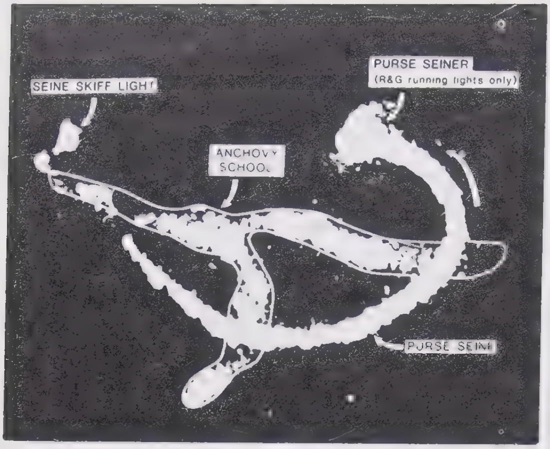


Figure 1. Bioluminescence of an anchovy school, purse seiner, and net recorded by a low-light-level video system. Photo taken by author during anchovy surveys off northwest Mexico, courtesy Zapata Fisheries Development Corporation (altitude - 1,828 meters (6,000 ft)).

The National Marine Fisheries Service's (NMFS) Southwest Fisheries Center has expended considerable effort over the years in the study of detection and profiling of fish school targets using acoustic techniques (Smith, 1970; Hewitt et al., 1976). Studies of the horizontal profiles of fish school targets have been made with aerial photographs and a low-light-level video system (Squire, 1978). Recently underwater laser-radar experiments on fish targets were conducted under laboratory conditions by the Swedish National Board of Fisheries (K. Fredriksson et al., 1978). These studies were preliminary to field tests planned on board a research vessel. The National Marine Fisheries Service has recognized the possibility of using technologically advanced airborne survey aids such as the optical laser, and has conducted a limited amount of experimental studies concerning the reflectance of fish. However the development of such an airborne optical laser system suitable for routine fishery surveys would require funding a research and development expertise currently beyond the capability of the Service.

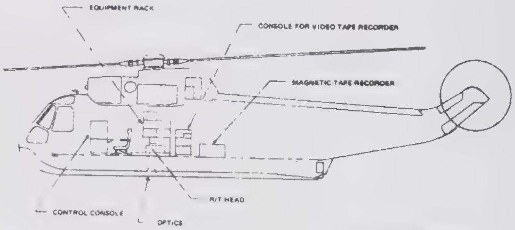
As in other areas of underwater research, the development of electronic survey equipment for one specific use may find application in other related fields. The observation of a fish school as reported in this paper is an example of a cooperative effort between NAVAIRDEVCEN, Warminister, Pennsylvania, and the NMFS Southwest Fisheries Center, La Jolla, California, relative to making observations of fish school targets intercepted during airborne tests of the ORIC system. Targets such as fish schools were of interest to the ORIC program and records of fish school targets intercepted were made available to the Southwest Fisheries Center.

The mounting of electronic sensors in an aircraft capable of detecting and measuring fish school parameters provides a capability of surveying large areas of the ocean's surface within a shorter time period than can be done from abroad ship. Advanced electronic detection and measuring devices are being developed. Optical laser radar, for example, offers a new capability in the field of fish school detection and evaluation. In 1962, the U.S. Navy initiated a program at the Naval Air Development Center (NAVAIRDEVCEN) to determine the feasibility of sursurface target detection using a pulsed optical laser system. This program was initially identified as the ORAD (Optical Ranging and Detection) program; the acronym ORIC (Optical Ranging, I.F.F., and Communications) was later adopted. The objective of this program was the development of an operationally useful airborne laser radar system capable of detecting submerged targets. In 1963-1965 the feasibility of using a pulsed laser for underwater ranging was demonstrated. Development has continued and more sophisticated optical laser scanning systems have been tested.

RESULTS

Observation #1

In November-December 1976, tests of ORIC system mounted in an SH-3 helicopter (Figure 2) were conducted in the Key West Florida area. During these tests



SH-3 Helicopter

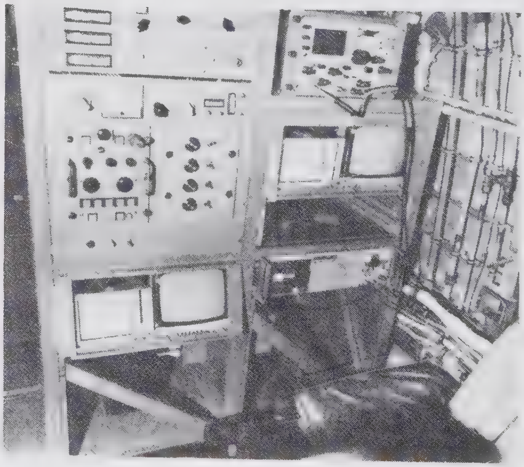


Figure 2. Positioning of ORIC components in SH-3 helicopter and view of operator's console.

possible fish targets were indicated in an area approximately 12 nautical miles south of Key West. During some of the test flights, spurious signals were detected. Since these signals were present only on the backscatter curves, which are a function of water reflectance and exponentially decaying laser power, it is assumed that the signals were due to fish.

A series of oscilloscope photographs was obtained showing laser return signals from fish. This series of photographs (one is shown in Figure 3) was obtained approximately 1 minute before passing over the test target. For a nominal aircraft speed of 60 knots, this places the fish approximately 1 mile from the target. The data block on each photograph contains a shot number, a laser peak power measurement, and aircraft radar altitude. Date and takeoff time as well as oscilloscope scale factors are also given. Laser scan angle and beam divergence are data not indicated on the photographs; the fixed unstabilized scan angle was 45° and beam divergence was 48 mr. Because of this combination, target depth cannot be readily obtained. The range of possible depths, however, is surface to 11 meters (36 ft). Since depth and reflectivity are unknown, it is not possible to determine the size of the target.

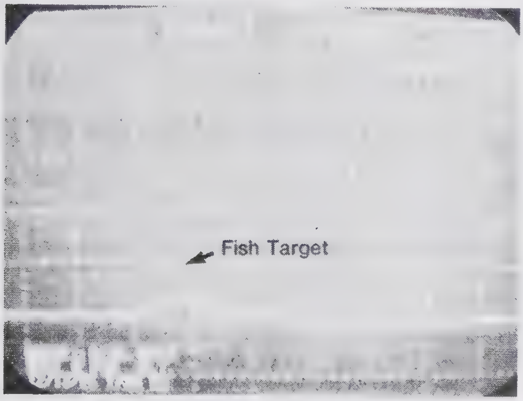


Figure 3. Oscilloscope photograph showing laser return signal from fish near the surface (surface to 11 meters (36 ft)).

Sample calculations show that a target on the surface with a cross section of 1 square foot and a reflectivity of 50 percent would produce a return similar to those in the photographs. The width of the return signals shows little pulse spreading, which is characteristic of targets near the surface. No visual confirmation was possible due to lighting conditions during the flight which was conducted at dusk and during the night.

Observation #2

During tests of the ORIC optical system on December 6, 1977 a small school of fish was detected. This detection occurred near the Five Fathom Bank about 8 miles east of Wildwood, New Jersey. The ground speed of the SH-3 helicopter carrying the ORIC equipment was 60 knots and the altitude was 152 meters (500 ft). The pulse repetition rate of the laser was 15 Hz.

Figure 4 is an intensity modulated record of this detection. This record was made from the flight test magnetic tape recording using a modified Tektronix 4631 hard copy unit. The depth scale shows the bottom depth to range from 9.1 to 12.2 meters (30 to 40 ft). The arrow points to the return signal from the fish school. This return also shows some variation in depth and a shadowing that reduced the return from the bottom.

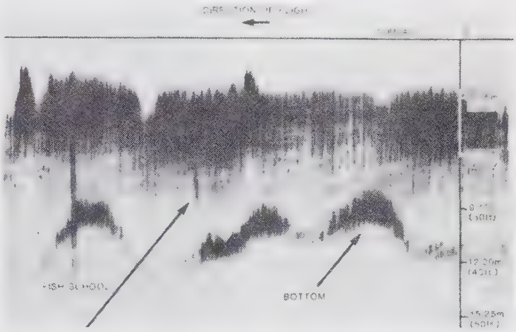


Figure 4. An intensity modulated record of a fish school detected over Five Fathom Bank off Wildwood, New Jersey on December 6, 1977. Arrow indicates direction of fish school plot appearing in Figure 6.

Figure 5 is a photograph of a pseudo "3D" display showing the same signals. The fish school and the bottom can be readily identified in this photograph.

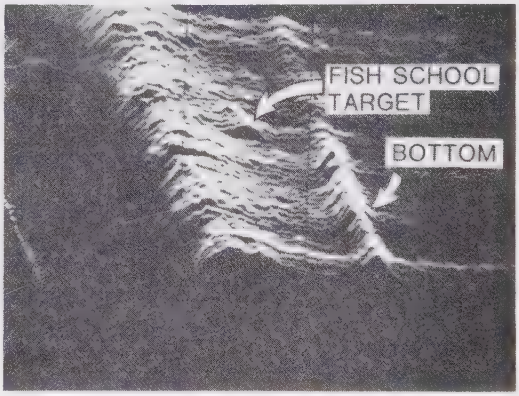


Figure 5. A "3D" oscilloscope display showing the fish school and ocean bottom.

A vertical profile of the fish school target was plotted (Figure 6) based on pulse rate, return width and rate of aircraft movement over the surface (ground speed). The length of the school profile, as measured through a portion of the school by the vertical looking laser beam, was approximately 28.8 meters (87.8 ft) by 2.62 meters (8 ft) at maximum thickness. Thirteen target intercepts were recorded over a 28.8 meter section of the school. The upper and lower boundary of the school was 7.1 meters (21.5 ft) and 9.7 meters (29.5 ft) below the surface, respectively.

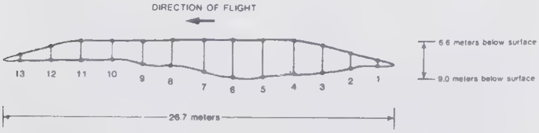


Figure 6. Vertical cross-section of a portion of the fish school directed by the optical laser and plotted from the intensity-modulated record. Length of intercept 26.7 meters (87.5 ft) calculated from a pulse rate of 2.06 meters (6.75 ft) per pulse × 13 pulse intercepts. Arrow indicates direction of plot as observed in Figure 4.

The species of fish intercepted is unknown and no visual observations were attempted. Water clarity in the area was not measured but was reported to be typical of the region. For this area Secchi disk depths are reported to average < 10 meters.

DISCUSSION

Assessment of pelagic near-surface schooling fishery resources requires the detection of fish schools and their measurement in both the horizontal and vertical planes. The photographic and electronic techniques currently in use are capable of profiling in the horizontal plane only. Aerial photos can profile the school in the horizontal plane if lighting conditions are optimum, and the fish school is near the surface and turbidity levels are near optimum for photography. LLTV systems also produce a profile in the horizontal plane. The LLTV system should be capable of providing species identification resulting from the differential behavior patterns displayed when the individual fish are subjected to pulsed light. These systems can detect bioluminescence generated by fish school action on or near the surface and at considerable depths, dependent upon turbidity levels and the concentration of bioluminescing organisms.

Optical lasers offer an unexplored potential because they can profile in both horizontal and vertical plane and are capable of operation during both daylight and darkness. An optical laser can be operated at high altitudes in a scanning mode thereby making it an effective airborne survey device. Airborne optical laser systems are currenlty being developed by the U.S. Navy to provide operational devices to obtain bathymetric data. These systems could be programmed for fish school detection. Detection depths are dependent upon water clarity, and may range to 75 meters (228 ft) or more; in coastal water of reasonable clarity, target detection depths should extend to at least 30 meters (91 ft).

In the future, airborne detection and profiling of pelagic fish schools using an airborne optical laser will play an important part in assessment of pelagic resources. Optical lasers and other airborne detection and identification devices such as LLTV, coupled with surface surveys using acoustical and fish sampling techniques, will contribute to a better understanding of pelagic fish resources.

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ESTIMATE OF THE SPAWNING BIOMASS OF THE NORTHERN ANCHOVY CENTRAL SUBPOPULATION FOR THE 1980-81 FISHING SEASON

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ABSTRACT

The spawning biomass of the central subpopulation of northern anchovies off the Pacific coast of the State of California and Northern Baja California was surveyed by four ichthyoplankton cruises during the period, February-May 1980. The extent of the 1980 coverage was about half of the four cruise surveys conducted in previous years. Using a modified larva census method, the estimate of the 1980 spawning biomass was calculated at 1,775,000 tons. The optimum yield (OY) for the 1980-81 fishing season within the U.S. Fishery Conservation Zone was 179,000 short tons as determined by the OY formulation adopted by the Pacific Fishery Management Council's Anchovy Plan. The 1980-81 U.S. reduction quota for the northern anchovy was set at 166,400 short tons. In the fall of 1980 the California Fish and Game Commission established an 80,000 short ton limit on the amount of anchovy that could be processed by shore-based reduction plants in California.

RESUMEN

La biomasa del desove para la subpoblación central de anchovetas del norte frente a la costa Pacífica del estado de California y de Baja California Norte fue estudiado durante cuatro cruceros de reconocimiento de ictioplancton durante febrero-mayo de 1980. El área cubierta en 1980 era aproximadamente la mitad de ésa cubierta en los cuatro cruceros de reconocimiento efectuados en años previos. Usando un método de censo de larva modificado, la estimación de la biomasa del desove para 1980 se calculó en 1,775,000 toneladas cortas. El rendimiento óptimo para la temporada de pesca 1980-81 dentro de la Zona de Conservación de Pesquería de los EE.UU. fue de 179,000 toneladas cortas, determinado por la formulación del rendimiento óptimo adoptada por el Pacific Fishery Management Council en su Plan para Anchoveta. La cuota de reducción de los EE.UU. para 1980-81 para la anchoveta fue fijada en 166,400 toneladas cortas. En el otoño de 1980 la Comisión de Pezca y Caza de California estableció un límite de 80,000 toneladas cortas para la cantidad de anchoveta que podía ser procesada por las plantas de reducción basadas en las costas de California.

INTRODUCTION

Catch quotas for the U.S. anchovy fisheries are established each year on July 1 using the current estimate of the anchovy spawning biomass as specified by the formulation in the Fishery Management Plan (FMP) for the Northern Anchovy Fishery (Pacific Fishery Management Council 1978). This paper is the third in a series of reports that document the annual estimate of spawning biomass of the central subpopulation of northern anchovy from which the optimum yield for the coming season is established (Stauffer and Parker 1980; and Stauffer 1980). The 1980 estimate is based on anchovy larva abundance data collected on the 1980 California Cooperative Oceanic Fisheries Investigations (CalCOFI) egg and larva survey of four cruises that only partially surveyed the seasonal and areal range of the northern anchovy spawning period. This survey was conducted under the direction of the La Jolla Laboratory, Southwest Fisheries Center (SWFC), National Marine Fisheries Service. Other research institutions cooperating in this survey were the Scripps Institution of Oceanography, Instituto Nacional de Pesca, Mexico, and Pacific Research Institute of Fisheries and Oceanography, Soviet Union.

LARVA SURVEY

Anchovy spawning biomass was estimated from anchovy larva abundance using a modification of the larva census method developed by Smith (1972) and further documented in Appendix I of the FMP (PFMC 1978). The incomplete larva census estimates for winter and spring quarter, which resulted from the partial coverage of the survey, were expanded to an annual larva census based on a regression analysis of the historical CalCOFI data. The four cruises on the egg and larva survey were conducted within the geographic range of the central subpopulation of the northern anchovy (Vrooman et al. 1980) as outlined by the eight regions shown on the CalCOFI station plan given in Figure 1.

The regions of southern California and Baja

[Manuscript received 8 June 1981.]

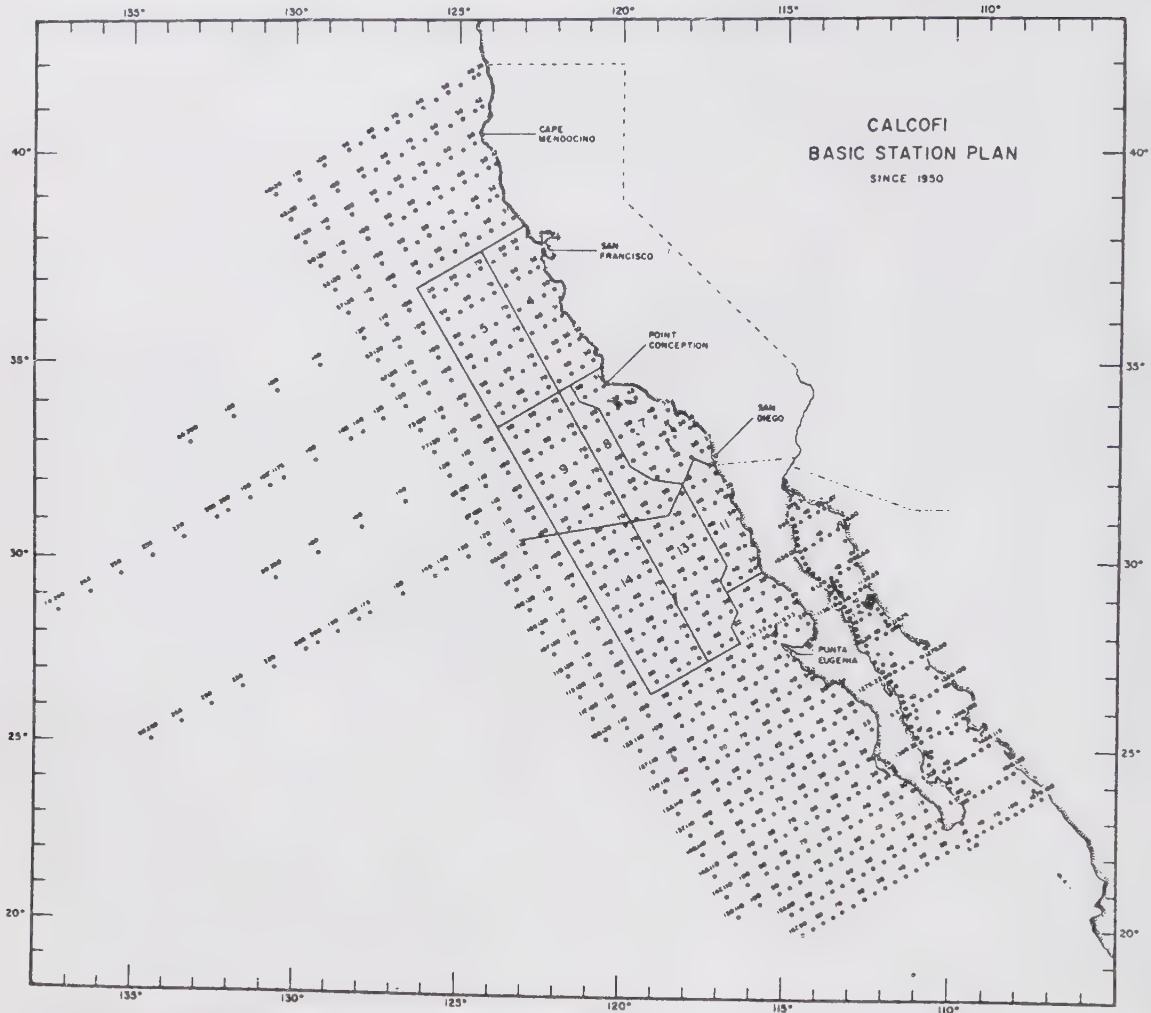

Figure 1. CalCOFI basic station plan. Geographic range of the central subpopulation of northern anchovy is within the light-numbered regions.

California were redefined so that the boundaries between the region group 7, 8, and 9 and the region group 11, 13, and 14 coincided with the U.S.-Mexico border as in 1979 (Stauffer 1980). The four cruises were 1) 8003 TK, February 21-March 17; 2) 8003 JD, March 20-April 10; 3) 8004 JD, April 11-19; and 4) 8005 JD, May 16-30. The first cruise was conducted by the Soviet R/V *Tikhookeanskiy* and the other three by the U.S. R/V *David Starr Jordan*. The stations occupied by each cruise are shown in Figure 2. The occupied stations off central Caifornia for cruises 8004 JD and 8005 JD are not shown. Only one cruise 8003 JD received a permit to conduct fishery research within Mexico's 200-mile zone.

Collection and processing of anchovy larva samples in 1980 were the same as for the 1979 CalCOFI survey as reported by Stauffer (1980). Plankton samples were collected with the paired CalCOFI bongo net. The data and samples were brought back to the Southwest Fisheries Center (SWFC) for processing and sorting. All of the plankton sample from the starboard net was sorted if the station was beyond 200 miles or if the plankton volume was less than 26 ml; otherwise, a 50% aliquot of the sample was sorted. The 1980 estimate includes station data from only the 118 standard stations defined by Smith (1972) to be those stations routinely occupied since 1951 and within the range of the central subpopulation.

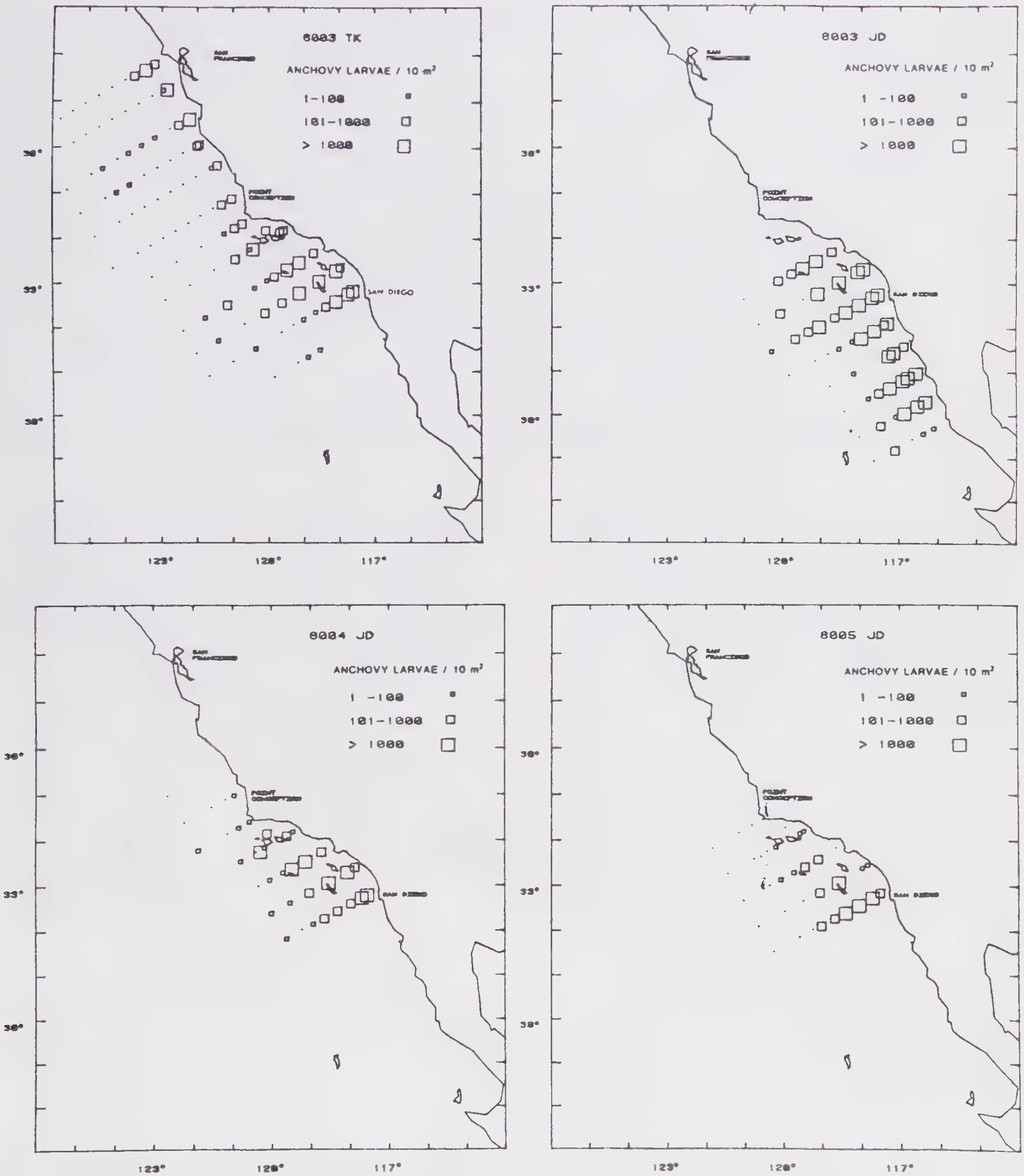

Figure 2. Pattern of occupied stations and geographic distribution of anchovy larvae for four CalCOFI cruises conducted during February-May period in 1980.

A decision was made in early winter 1980 to estimate spawning biomass also by the egg production method (Parker 1980) because of the limited coverage of the CalCOFI cruises. To accomplish the task, the 8003 JD and 8004 JD cruises were designed to include the collection of anchovy egg samples and adult fish with a midwater trawl net. Processing these samples in the laboratory was given first priority. There was insufficient time to process all bongo plankton samples to meet the July 1 deadline for announcement of the biomass estimate. As a result CalCOFI stations north of line 80 for cruises 8004 JD and 8005 were excluded from the processing and analysis.

In general the distribution of anchovy larvae for the central subpopulation was similar to that observed in 1979 for comparable regions and months (Stauffer 1980). The distribution of the standardized number of anchovy larvae per 10 M^2 sea-surface area is summarized in Figure 2 for the four 1980 CalCOFI cruises. For the Southern California Bight regions of 7, 8, and 9, larvae were within 140 nautical miles of the coast. The larva densities were highest in the Southern California Bight region 7 for the March and early April 8003 JD cruise with larva density tapering off by May similar to prior years. For central California regions samples were sorted for only the 8003 TK cruise conducted in early March. At this time anchovy larvae were distributed within 50 nautical miles of the coast. Examination of the anchovy egg samples from 8004 JD for central California regions found only a few anchovy eggs in Monterey Bay, suggesting that anchovy spawning had ceased in that area by the time of the 8004 JD cruise (Stauffer and Picquelle 1980). The distribution of anchovy larvae off northern Baja California extended about 100 nautical miles offshore, although the spawning apparently was concentrated within 40 nautical miles of the coast (Stauffer and Picquelle 1980).

Because the 1980 egg and larva survey lacked a January cruise and samples for CalCOFI northern Baja and central California regions in the spring quarter were not sorted, the 1980 annual larva census estimate was derived from a regression analysis of the historical CalCOFI anchovy larva data recompiled to generate larva census numbers that matched the coverage of the 1980 egg and larva survey (Table 1). The historical larva data were summarized for CalCOFI regions 7, 8, 9, 11, and 13 (southern California and northern Baja California regions) for the second half of the winter quarter (15 February to 31 March) and for regions 7, 8, and 9 for the spring quarter. These regions and time periods corresponded to areas in which 1980 CalCOFI larva samples were collected and sorted. These winter and spring totals were summed to provide a modified larva census (L_m) for the CalCOFI time series which was comparable to the incomplete larva census for the 1980 survey. To expand L_m to an equivalent annual larva census values (L_a) as given in Appendix I of the FMP, the difference between these values, L_u (i.e. $L_u = L_a - L_m$) was regressed on L_m for the historical CalCOFI years in which there were sufficient data (see Table 1). The analysis excluded the 1979 census data which was also an expanded estimate from a partial survey. This regression is

$$L_u = 3.043 - 0.0107\, L_m \qquad (1)$$

TABLE 1

Larva Census Data (10^9 Larvae) for Estimating 1980 Spawning Biomass

Year	(1) 2nd half of winter (Region 7,8,9,11,13)	(2) Spring quarter (Region 7,8,9)	Sum (1)+(2)	Annual larva census[1]	Estimated biomass[1] (1,000 tons)
1951	455	458	913	1,841	180
52	353	257	610	1,600	156
53	1,705	144	1,849	5,208	510
54	3,730	410	4,140	7,838	768
55	5,644	1,047	6,691	8,618	846
1956	3,506	816	4,322	4,944	485
57	4,192	4,027	8,219	11,960	1,172
58	5,203	3,620	8,823	15,087	1,479
59	3,825	4,843	8,668	15,440	1,514
60	10,527	4,804	15,331	15,713	1,540
1966	14,170	17,212	31,382	36,452	3,572
1969	32,852	3,496	36,348	30,594	2,998
1972	14,359	6,857	21,216	28,373	2,781
1975	27,563	387	27,950	36,768	3,603
1978	10,994	2,630	13,624	13,306[2]	1,304[2]
79	10,111	3,612	13,723	17,580[3]	1,723[3]
80	11,830	3,400	15,230		1,775

[1] Source: Appendix I of Northern Anchovy FMP (PFMC 1978)

[2] Stauffer and Parker 1980

[3] Stauffer 1980

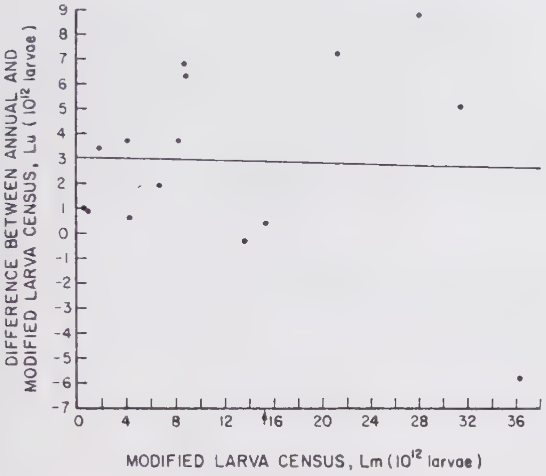

Figure 3. The regression model for expanding the modified larva census, L_m, to the annual larva census, L_a.

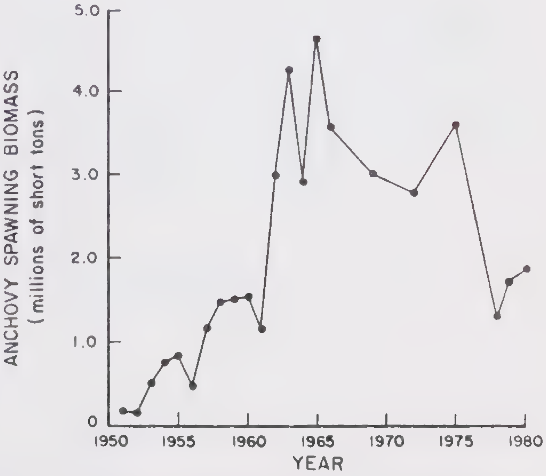

Figure 4. Estimated spawning biomass for the central subpopulation of northern anchovies, 1951-80.

and is shown in Figure 3. Although the slope (−0.0107) is not significantly different from zero, equation (1) was used to estimate L_u for 1980. The incomplete winter and spring larva census numbers for 1980 were 11,830 × 10^9 and 3,400 × 10^9 larva. These values are quite similar to the recompiled 1978 and 1979 larva census numbers. The sum of 1980 winter and spring numbers gives L_m value of 15,230 × 10^9 larvae. From (1) the 1980 value of L_u is 2,880 × 10^9 larvae. Approximate 95% confidence limits for $L_u \pm$ are 8.400 × 10^9 larvae. The equivalent annual larva census value, L_a, for 1980 is 18,110 × 10^9 larvae, the sum of L_u and L_m.

The estimate of the 1980 anchovy spawning biomass for the central subpopulation, using the larva census method developed by Smith (1972)

$$B = 9.8 \times 10^{-8} L_a,$$

is 1,775,000 short tons for L_a equal to 18,100 × 10^9 larvae. Stauffer and Picquelle (1980) using the new egg production method (Parker 1980) estimated the 1980 anchovy spawning biomass to be 942,100 short tons. However, the larva census estimate is the appropriate estimate for setting the 1980 harvest quota by the procedure set forth in the anchovy FMP, since the model used in the evaluation of the harvest policy was dependent on the historical larva census estimates of anchovy biomass. Based on the larva census method, the 1980 anchovy spawning biomass is relatively unchanged from the 1979 level of 1,723,000 tons (Stauffer 1980). Optimum yield for the central subpopulation during 1980–81 season as specified in the FMP was 255,750 short tons. Within the U.S. Fisheries Conservation Zone the optimum yield was 179,400 short tons with a U.S. anchovy reduction quota set at 166,400 short tons. Because of the concern for the status of the anchovy resource arising from the egg production estimate of less than 1,000,000 tons, the California Fish and Game Commission in the fall of 1980 established an 80,000 short ton limit on the amount of northern anchovy that could be processed by shore-based reduction plants in California. The Commission's action included a provision for considering future increase if the reduction plants approach the 80,000 ton limit.

ACKNOWLEDGMENTS

The collection and processing of the egg and larva data for this biomass estimate depend on the cooperation of many people on the staff of Southwest Fisheries Service (SWFC), Scripps Institution of Oceanography (SIO), Instituto Nacional de Pesca, NOAA ship R/V *David Starr Jordan* and USSR R/V *Tikhookeanskiy*. Some of the data were collected under the authority of the Secretaria de Relaciones Exteriores and the Departamento de Pesca of Mexico. I especially thank the SIO plankton sorting group and James Thrailkill, Richard Charter, Oden Burris, William Flerx, Dimitry Abramenkoff, and Jack Meteyor of SWFC. We also thank Daniel Huppert and Alec MacCall of California Department of Fish and Game for their suggestions and review.

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TUNAS AND THEIR ENVIRONMENT IN THE PACIFIC OCEAN: A REVIEW

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INTRODUCTION

Fifteen years ago, the late Harold Barnes invited one of us to review relations between tunas and their oceanic environment in this Annual Review Series (Blackburn, 1965). Recent advances in that field prompted the U.S. National Marine Fisheries Service to commission the writing of an updated review for the benefit of investigators in all countries. The present paper is the result of that work. Tunas are of increasing interest to marine scientists in a number of ways: as food resources, as pelagic organisms with immense but well-described distributions, as apex predators in oceanic ecosystems, and as a group of fishes with unique anatomy, biochemistry and physiology. These interests have led to the mounting of oceanographic expeditions and the founding of scientific organizations, many of them multi-disciplinary or international. From those and other efforts, tuna ecology has progressed from the descriptive to the explanatory phase, although much work of both kinds still remains to be done. Designed experiments have become frequent. The making and testing of fairly complex models has begun. This progress is summarized and reviewed here. Probably no group of oceanic animals has been the subject of such comprehensive ecological research on a world scale, except perhaps cetaceans. Many valuable contributions to the mainstream of oceanography have resulted from tuna-ecological programmes, although they are not within the scope of this review. Examples include the discovery of the Pacific Equatorial Undercurrent (Cromwell, Montgomery & Stroup, 1954), and the development of a method for the continuous measurement of *in vivo* chlorophyll concentration (Lorenzen, 1966). At present work continues notably in the areas of physiology, behaviour, biochemistry, genetics, stock identification, and fluctuations in distribution and abundance, as well as on refinement of recent definitions of species habitat.

Major compilations of information on tuna ecology have been made. Of particular note are the works collected in the Symposium on Scombroid Fishes, Parts 1–4, Mandapam Camp, India (Anonymous, 1962); the Proceedings of the World Scientific Meeting on the Biology of Tunas and Related Species, Vols. 1–4, FAO Fisheries Report No. 6 (Rosa, 1963); Proceedings of the Governor's Conference on Central Pacific Fishery Resources, Honolulu, U.S.A. (Manar, 1966); and the review mentioned above (Blackburn, 1965). We intend not to consider the material covered in these works in detail, but rather to concentrate on reviewing the progress made in understanding tuna-environment interrelationships since then. The greater part of this review relates to six tunas (yellowfin, skipjack, bigeye, albacore, bluefin, and southern bluefin) and to one ocean, the Pacific. References to other species and oceans are restricted to those most necessary for the understanding of the subject. In our discussions of the impact of the environment on the tunas we shall confine our remarks mostly to the influence of features on distribution, and not on abundance. Real abundance cannot be determined at this time, and descriptions of stocks and changes in their condition (abundance) are speculative.

NOMENCLATURE

The six species selected for primary consideration in this paper are the tunas which have been exploited commercially. Because of their commercial importance they have been subjects of research investigations to varying degrees. All species discussed are in the family Scombridae, which was reviewed by Collette & Gibbs (1963), and commonly are called tunas in the English vernacular. More recently Klawe (1977) summarized the classification of the family and discussed the common and scientific nomenclature. Sharp & Pirages (1978) discussed the phylogenetic relationships among the tunas. In this paper references to the six principal tunas will be made according to:

Scientific Nomenclature	Vernacular Nomenclature
Thunnus alalunga (Bonnaterre)	Albacore
Thunnus albacares (Bonnaterre)	Yellowfin
Thunnus maccoyii (Castelnau)	Southern bluefin
Thunnus obesus (Lowe)	Bigeye
Thunnus thynnus orientalis (Temminck and Schlegel)	Bluefin: Northern (Pacific)
Katsuwonus pelamis (Linnaeus)	Skipjack

Other species are named where they occur in the text.

AREAL DISTRIBUTION OF PACIFIC TUNAS

Our knowledge of geographical ranges of the principal tuna species now appears to be almost complete in all oceans. Few large extensions of range have been reported during the past fifteen years. Here we summarize information on areal distribution of adult tunas, as distinct from that of tuna larvae. We consider as adults all ontogenetic stages at which the fish resemble adults morphologically, regardless of size or sexual condition. There is not much information about such stages at sizes below 30 cm, which are known mostly from stomach contents of larger fish (Yoshida, 1971; Mori, 1972).

The principal sources of information on adult distribution are records of commercial fisheries and fishery research surveys. The latter are important sources in areas where fisheries have not developed. Commercial fisheries are of three main types, surface hooking (mostly pole-and-line fishing, trolling), surface netting (mostly purse-seining), and subsurface hooking (pelagic long-lining); or more simply of two types, surface and subsurface. Surface fisheries are more restricted in area than subsurface, partly because they need high concentrations of visible fish and also because of special conditions such as bait supply, weather, and market demand. They can expand when the special conditions change or are overcome, as has recently occurred with the introduction of larger and faster vessels to fish yellowfin and skipjack in the eastern tropical Pacific. Individuals of a particular species caught in surface

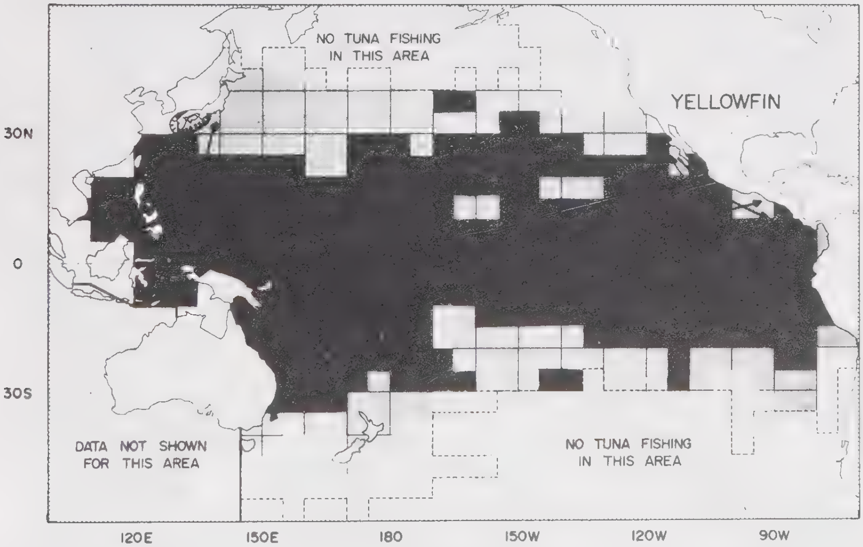

Fig. 1.—Distribution and movements of yellowfin tuna in the Pacific Ocean: broken lines shown are extreme poleward boundaries of the Japanese longline fishery in the years 1971–1977; within that area, heavy shading shows 5-degree rectangles in which the longline catch of yellowfin was ⩾0·5 fish per 100 hooks in any quarter-year; light shading indicates a catch rate lower than that; open areas indicate zero catch; hatched lines are approximate boundaries of surface fishing areas for yellowfin, which are explained further in the text; arrows (schematic) show major movements of tagged and recaptured yellowfin.

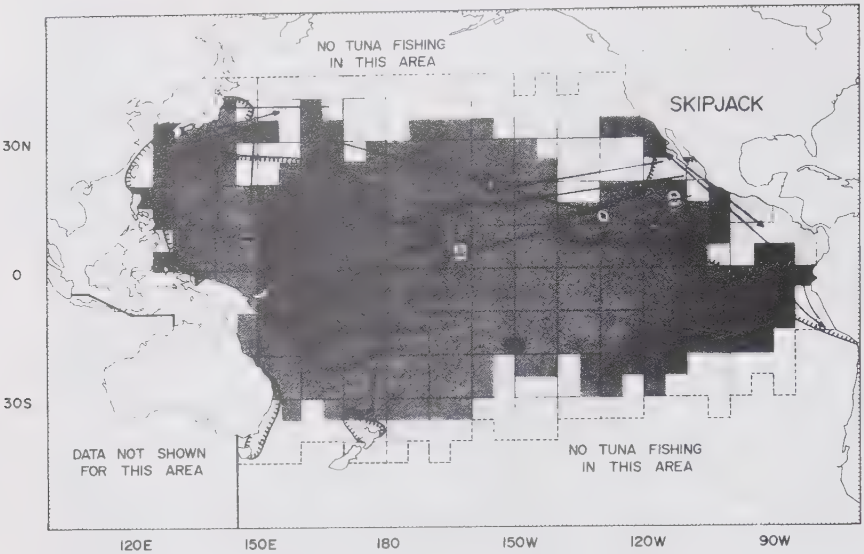

Fig. 2.—Distribution and movements of skipjack tuna in the Pacific Ocean: broken lines shown are extreme poleward boundaries of the Japanese longline fishery in the years 1964–1967; within that area, heavy shading shows 5-degree rectangles in which the number of skipjack caught per 100 hooks was two or more times the average for the whole area, in any quarter-year; light shading indicates a catch rate lower than that; open areas indicate zero catch (from Matsumoto, 1975); hatched lines are approximate boundaries of surface fishing areas for skipjack, which are explained further in the text; arrows (schematic) show most extensive movements of tagged and recaptured skipjack; note arrow (ee) indicating movement from approximately 110° W: 15° N to 167° W:3° N is in error and should be disregarded (W. Bayliff, pers. comm.).

fisheries tend to be smaller than in subsurface fisheries. Higgins (1966) summarized data on that subject for yellowfin, bigeye, and albacore, and Robins (1963) gave similar information for southern bluefin. Skipjack are caught only incidentally in subsurface fishing, but large skipjack are possibly more common below than at the surface (see p. 485).

Figures 1 to 5 show the limits of range in the Pacific of yellowfin, skipjack, bigeye, albacore, and bluefin from the records of the Japanese long-line fishery, and Figure 6 shows worldwide limits for southern bluefin from the same fishery. Except for skipjack these charts are based upon records published by the Research Division, Fisheries Agency of Japan, for the years 1971 to 1977, which are the latest available. The charts for skipjack are based upon records for the years 1964 to 1967, assembled by Matsumoto (1975). Areas where there was no long-line fishing in any of those years are indicated. In Figures 1 to 4, areas of higher and lower relative abundance, measured by catch per unit of fishing effort, are distinguished. Figures 1 to 6 also show approximate boundaries of areas of surface fishing, based on information from the following sources: for yellowfin, Schaefer, Broadhead & Orange (1963) and Suzuki, Tomlinson & Honma (1978); for skipjack,

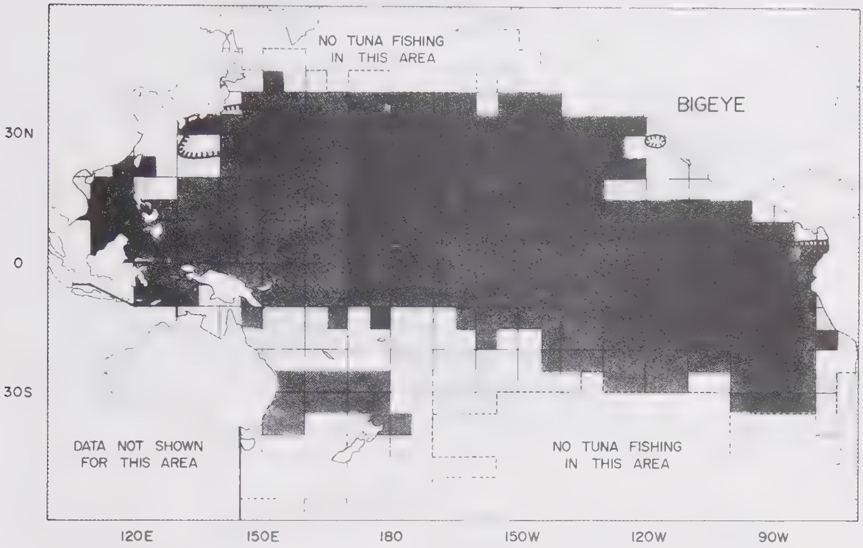
NO TUNA FISHING IN THIS AREA
BIGEYE
30N
0
30S
DATA NOT SHOWN FOR THIS AREA
NO TUNA FISHING IN THIS AREA
120E
150E
180
150W
120W
90W

Fig. 3.—Distribution of bigeye tuna in the Pacific Ocean: broken lines shown are extreme poleward boundaries of the Japanese longline fishery in the years 1971–1977; within that area, heavy shading shows 5-degree rectangles in which the longline catch of bigeye was ⩾0·5 fish per 100 hooks in any quarter-year; light shading indicates a catch rate lower than that; open areas indicate zero catch; hatched lines are approximate boundaries of surface fishing areas for bigeye; the arrow (schematic) shows the most extensive movement of a tagged and recaptured bigeye.

Matsumoto (1975), Otsu (1975), and Inter-American Tropical Tuna Commission (1978); for bigeye, Barrett & Kume (1965) and Kume & Morita (1967); for albacore, Yoshida & Otsu (1963); for bluefin, Bell (1963, unpubl.), Yamanaka & staff (1963), I. Yamanaka (pers. comm.), and Bayliff & Calkins (1979); and for southern bluefin, Robins (1963). We have also referred to Joseph, Klawe & Murphy (1979).

Yellowfin, skipjack, bigeye, and albacore are similar in their total range in the long-line fishery, namely about 40° N to 40° S in the Pacific (Figs 1 to 4). Comparing distributions at two levels of relative abundance shows, however, important differences between some of these species. Yellowfin is the most tropical of the four species, being most abundant between 30° N and 30° S. Skipjack and bigeye are relatively abundant from the Equator to about 35° or 40° in each hemisphere. Albacore has a comparatively low relative abundance in equatorial waters, and its poleward limits are at slightly higher latitudes than bigeye. All four species are relatively scarce in certain parts of the eastern tropical Pacific, for reasons discussed later (see pp. 480–487) under temperature and oxygen. Bluefin (Fig. 5) occur principally at about 25° to 35° in the North and South Pacific and also in equatorial waters of the western Pacific. Except for the surface fishery area off the Californias, the species seems less common east than west of 155° W, especially in the tropical region. Individuals have been recorded as far north as 57° N in the Pacific. Bluefin extend as far south as 15° to 20° S in the western Pacific (Shingu,

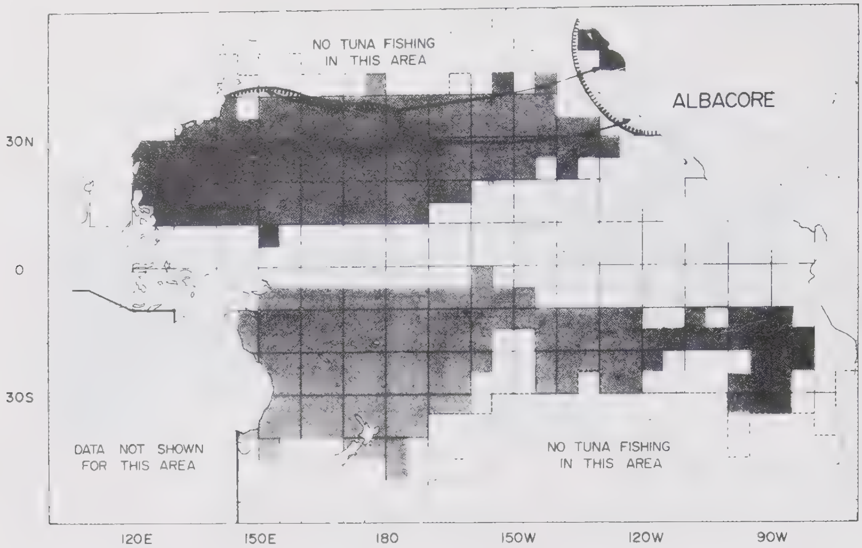
NO TUNA FISHING IN THIS AREA
ALBACORE
30N
0
30S
DATA NOT SHOWN FOR THIS AREA
NO TUNA FISHING IN THIS AREA
120E
150E
180
150W
120W
90W

Fig. 4.—Distribution and movements of albacore tuna in the Pacific Ocean: broken lines shown are extreme poleward boundaries of the Japanese longline fishery in the years 1971–1977; within that area, heavy shading shows 5-degree rectangles in which the longline catch of albacore was ⩾0·5 fish per 100 hooks in any quarter-year; light shading indicates a catch rate lower than that; open areas indicate zero catch; hatched lines shown are approximate boundaries of surface fishing areas for albacore; arrows (schematic) indicate generalized movements of tagged and recaptured albacore.

Warashina & Matsuzaki, 1974), and longline records show the apparent occurrence of bluefin in the area of 5° to 15° S, 90° to 135° W (Fig. 5). Long-line records also indicate their occurrence from 20° S to 50° S off eastern Australia, New Zealand, and from 25° to 35° S off Chile. The point has been made that these fish may instead be southern bluefin, but Japanese fishermen are considered to be accurate in separating the two bluefin species (in view of the significant difference in market value). Southern bluefin (Fig. 6) occurs between 10° and 55° S overall, and abundantly from 25° to 50° S in the Pacific. The apparent gap in its distribution in the South Pacific, between 100° and 155° W, may reflect the lack of any fishing in that region. The range of this species in other oceans is similar, except in the eastern Indian Ocean where it is also abundant from 5° to 25° S.

The surface fishing areas fall within the ranges for the long-line fishery except for certain coastal waters. Those for some species require comment. The surface fishery for yellowfin and skipjack in the eastern Pacific now extends nearly half way across the ocean (Figs 1 and 2), but until 1968 it operated only within a relatively narrow band, up to 500 km wide, adjacent and parallel to the American coast. Most of the catch taken west of 115° W is yellowfin, which is the higher-priced species and the easier species to take by purse-seining because of its association with porpoise (Calkins, 1975; Perrin, 1975; Suzuki *et al.*, 1978). The range of surface yellowfin in the eastern and central tropical Pacific is more extensive than shown, because the species

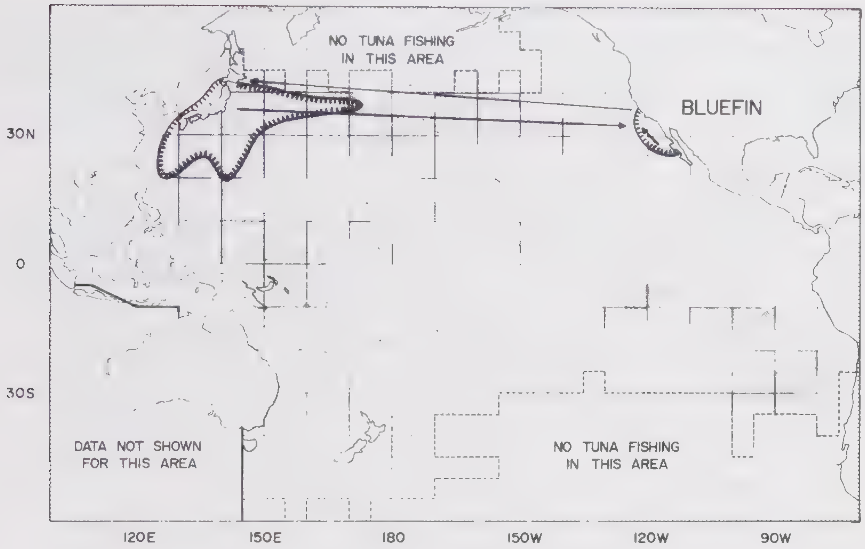

Fig. 5.—Distribution and movements of bluefin tuna in the Pacific Ocean: broken lines shown are extreme poleward boundaries of the Japanese longline fishery in the years 1971–1977; within that area, shading shows 5-degree rectangles in which any bluefin were taken; hatched lines shown are approximate boundaries of surface fishing areas for bluefin; arrows (schematic) indicate generalized movements of tagged and recaptured bluefin.

has been taken by trolling and seen in schools during research cruises in several other areas, especially near islands. The same cruises likewise demonstrated a much wider distribution of skipjack than the surface fishing areas shown. The skipjack were less confined to island regions than yellowfin, and were more abundant than yellowfin except near certain islands (Murphy & Ikehara, 1955; Murphy & Shomura, 1972; Blackburn & Williams, 1975). Some of the skipjack surface fisheries in the western tropical Pacific

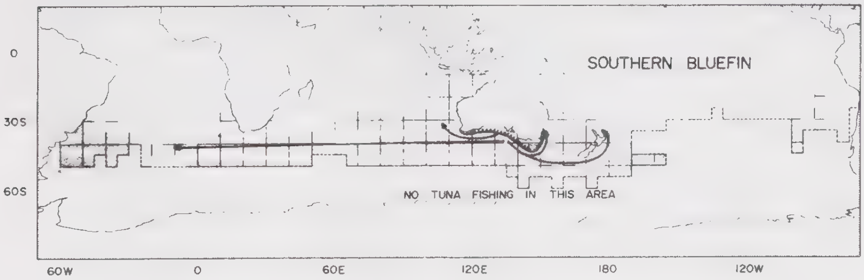

Fig. 6.—Distribution and movements of southern bluefin in all oceans: broken line shown is the extreme southern boundary of the Japanese longline fishery in the years 1971–1977; within that area, shading shows 5-degree rectangles in which any southern bluefin were taken; hatched line shown is the approximate boundary of the surface fishing area for southern bluefin; arrows (schematic) show major movements of tagged and recaptured southern bluefin.

have recently extended their range (Otsu, 1975). The area shown off eastern Australia in Figure 2 is the known range of surface skipjack in coastal waters, not of the fishery which is very small because of low demand locally (Blackburn & Serventy, in press). The area shown off New Zealand is according to Habib (1976). Surface fishing areas for bigeye are quite restricted (Fig. 3) and only small catches are made there.

The distributions shown in Figures 1 to 6 are discussed later (see pp. 480–500) in relation to particular ocean conditions that may determine them. At this point, however, it is of interest to compare them with a series of biotic provinces recognized in the Pacific by McGowan (1974). These provinces are not based primarily on currents, water masses, or ocean properties, although they obviously are related to some of these. They were recognized empirically by classifying charted distributions of many species of pelagic organisms into a small number of distinct but overlapping patterns. Most of the organisms were zooplankton but some were nekton and phytoplankton. The provinces are Subarctic and Subantarctic (poleward of 40° N and S), North and South Transition (30° to 45° in each hemisphere), North and South Central (10° to 35° in each hemisphere, but tending to join across the Equator in the western Pacific), Equatorial (between 25° N and 25° S), and Eastern Tropical Pacific (between 20° N and 20° S in the eastern Pacific). In addition to the eight faunas respectively characteristic of these provinces, a Warm Water Cosmopolite fauna, ranging from about 40° N to 40° S, was recognized. The boundaries given apply to the areas in which over 60% of the species in the faunas occurred.

The distributions of albacore and northern bluefin show a reasonable congruence with the North and South Central provinces. The yellowfin distribution is somewhat like the Equatorial province but extends more poleward, whence this species could also be considered a Warm Water Cosmopolite. The area of the present surface fishery for yellowfin and skipjack in the Eastern Tropical Pacific is similar to McGowan's Eastern Tropical Pacific province. Southern bluefin occur mainly in the South Transition province but to some extent in subtropical and tropical waters as well. Skipjack and bigeye are clearly Warm Water Cosmopolites. Tunas have much greater mobility than the other organisms on which McGowan's scheme is based, so one would not necessarily expect them to conform to that scheme unless they were prey-selective for particular province faunas. In fact, they are opportunistic feeders (see p. 490).

The distributions of tunas or any pelagic species are, of course, contained within fluctuating natural boundaries and not by latitude and longitude. McGowan's (1974) paper is valuable in specifying a number of these natural faunal boundaries, although for various reasons, such as indicated later for the tunas, these boundaries will not apply to all species.

BATHYMETRIC DISTRIBUTION OF PACIFIC TUNAS

Information on the vertical distribution of tunas is based mostly upon estimates of depth of capture in commercial and/or research fishing operations. A few observations have been made by use of depth-indicating sonic tags, by maximum–minimum depth or temperature sensors, and by echo sounding.

On one occasion, observations were made from a submarine vehicle. It has been estimated that most hooks on a commercial longline hang at depths between 80 and 140 m (Yabuta & Ueyanagi, 1953), and a mean depth of 100 m has been assumed for certain purposes in this paper. Lines set in strong currents will not fish so deeply. Tuna can be caught while the line is sinking, at rest, or being retrieved.

The surface fisheries generally take smaller fish than those caught on longlines. In pole-and-line operations, and sometimes in trolling and purse seining, the fish appear at the sea surface. The deepest purse-seines, however, are effective at depths to 50–80 m and yellowfin are known to escape under such nets.

The depth range of a tuna species is not the same in all regions. For example, Hanamoto (1974) found that bigeye catch rates as a function of depth varied with latitudinal zones in the eastern tropical Pacific. He considered this variation to be related to zonal currents. Depths of capture for the different zones were:

Latitudinal Zone	Capture Depth
9° N–3° N	90–140 m
3° N–3° S	50–150 m
3° S–9° S	110–160 m
9° S–13° S	120–160 m

Longline catches vary in species composition depending on area and season, and it is shown later that some of these differences can be explained from vertical distributions of temperature and dissolved oxygen concentration.

Japanese workers have made several valuable observations on bathymetric distributions of Pacific tunas in recent years. Saito (1973) and Saito & Sasaki (1974) used special very deep lines, with depth recorders at the hooks, in an area west of Fiji. They obtained yellowfin, bigeye, and albacore down to 380 m, which was the greatest depth fished. The yellowfin and albacore seemed to be approaching the bottom of their range at 380 m, since they were most abundant at depths less than 300 m. On the other hand, the bigeye were most abundant at depths over 300 m. Suzuki, Warashina & Kishida (1977) compared catches of the regular longline, fishing to about 130 m, and of another type that fished to about 260 m. The ratios of mean catches by number of fish, deep: regular, were as follows:

yellowfin	0·73
albacore	0·82
bigeye	1·79

These observations indicate that abundance of bigeye increases below the depth of regular commercial longlines, whereas abundance of the other two species does not. Similarly, Hanamoto (1976) found that more bigeye were caught on the deepest hooks (160 m) of the regular longline than on the shallower hooks, which took more yellowfin. It is clear that we cannot yet specify the maximum depth of occurrence of bigeye with any certainty.

No similarly detailed bathymetric data are available for bluefin or southern bluefin, which are taken by longline as well as in surface fishing. The deepest records of skipjack are 185 m from a submersible (Anonymous, 1965) and 263 m from sonic tracking (Dizon, Brill & Yuen, 1978) (see Fig. 15). It is shown later that large skipjack are probably most abundant at subsurface levels.

MOVEMENTS AND SEASONAL DISTRIBUTION OF TUNA STOCKS

Tuna biologists have long suspected that some species are not homogeneous populations, but are groups of relatively independent sub-populations or stocks. The recognition of these stocks has begun in some species but is not complete in any. Stock definition is important for the management of fisheries, and tuna biologists are increasingly active in this field. Each stock is expected to occupy a definable area although the areas may overlap. The principal methods of stock recognition are tagging and statistical analysis of differences between measurable hereditary characters in samples of fish from different areas. Other biological observations can provide indications of the existence of separate stocks. For instance, the two spawning areas of albacore in the Pacific (Fig. 12) suggest reproductive isolation of northern and southern hemisphere stocks within that species.

Tuna schools or individual tuna move within the area of their stock. Tagging is the best source of information about these movements, some of which have been called migrations. Some authors (*e.g.*, Jones, 1968; Jones, Walker & Arnold, 1978) have defined migrations, as distinct from other movements of fishes. It is not easy, however, to apply their criteria to some of the movements that tunas have been found to make. As a result some tuna biologists have used the word "migration" quite loosely. In this paper we prefer the word "movement", and use "migration" only where necessary to agree with a cited author's use.

Nakamura (1954, 1969) hypothesized that tunas make two kinds of movements, which he called migrations: "One is assumed to be a rather passive movement within a certain habitat in response to a change in the conditions of the habitat, and the other as an active movement between habitats following a change in the physiological or ecological requirements of the fish." By habitat he meant a particular current system, usually zonal, as he considered that different species have their centres of distribution in different currents. His "migrations between habitats" were mostly meridional in direction, and seasonal in the examples given. Some of the "migrations within habitats", of which few examples were given, were also seasonal. Nakamura's central idea of characteristic habitats in different current systems has been criticized, as mentioned elsewhere, but there is direct and indirect evidence that tunas move zonally or meridionally or in both ways, seasonally in some instances.

There certainly is partitioning of energy in tunas between migration and spawning. Sharp (1978) defines several types of migrations, all related to feeding or reproduction. The first two types, short-term short-distance and long-term long-distance migrations, are facilitated by ocean currents or minor directed movements. They do not require much above basic energy needs and may represent the types which produce the spare energy needed for the subsequent spawning mode. The third type, short-term long-distance migrations, require the most energy (Sharp & Dotson, 1977), but may be the type which subsequently allows the very rapid growth needed for juveniles and pre-spawners. Sharp's classification does not include the case in which tunas move out of an area which is becoming unsuitable (such as by seasonal cooling). Seckel (1972) considered migration in a mechanistic sense. He described it as a combination of the movement of fish by virtue of their being carried by the current plus the movement of fish relative to the current. Seckel's hypothesis is further discussed in this section under Skipjack and on p. 489.

YELLOWFIN

Yellowfin movements in the Pacific have been demonstrated from tagging (Fig. 1 and Bayliff, 1979) and the distribution of fish contaminated by radioactivity, and inferred from changes in catch per unit of fishing effort between areas and seasons (Suzuki *et al*., 1978). The latter changes are not large and probably indicate movements due to currents within the gyres, or perhaps changes in fish concentration. The yellowfin movements are apparently less than ocean-wide in scale. Sharp (1972 and pers. comm.) biochemically recognized a lack of homogeneity within yellowfin of the eastern Pacific based on genetic disparities within some areas among age-cohorts. The longest predominantly zonal movement of a tagged yellowfin was about 3000 km (Bayliff & Rothschild, 1974; see large east to west arrow in Fig. 1). Meridional movements occur in the Kuroshio and California Currents (Suzuki *et al*., 1978 and references; Fink & Bayliff, 1970). They are seasonal, poleward in summer, with the Kuroshio and against the California Current. The movement in the California Current follows a shift in the 20 C surface isotherm, north in summer and south in autumn (Blackburn, 1969a). There is no evidence that any of these movements are for spawning. Spawning areas are widespread in the entire central area of adult yellowfin distribution, as shown in Figures 1 and 9.

SKIPJACK

Skipjack adults occur in most tropical waters right across the Pacific (Fig. 2). The spawning region is likewise tropical but less extensive, mostly west of 130° W (Fig. 10). Tagging has demonstrated that substantial movements should occur in a zonal direction between the American coastal region and the spawning areas (Fig. 2). A total of 24 fish tagged in the eastern Pacific have been recaptured in the central Pacific, including one that travelled at least 9000 km (Anonymous, 1979a). Other zonal movements of tagged skipjack have been observed within the central Pacific (Anonymous, 1979a). Tagging has also demonstrated meridional movements along the American coasts and in the Kuroshio Current (Fink & Bayliff, 1970; Anonymous, 1979a). Skipjack tagging programmes are operated by the Inter-American Tropical Tuna Commission, the South Pacific Commission, and various fishery organizations in Japan. Figure 2 shows the principal results. Some of the movement along the coast of North America is seasonal, the boundary of skipjack range moving first north and then south in step with the 20 C surface isotherm (Blackburn, 1969a; Williams, 1970). A similar seasonal change of range occurs off eastern Australia in conjunction with the 15 °C surface isotherm (Robins, 1952; Blackburn & Serventy, in press). The northward movement in the Kuroshio occurs through spring and summer (Kawai & Sasaki, 1962; Matsumoto, 1975 and references).

Population structure in Pacific skipjack has been studied from genetic analyses of blood group and serum group systems (Fujino, 1970a,b, 1972, 1976; Sharp, 1978). Fujino recognized two stocks or sub-populations, western and central-eastern, incompletely separated at about 160° to 170° E. Sharp recognized at least five overlapping stocks as shown in Figure 7, and more recently stated (pers. comm.) that there is evidence for at least one additional stock in the western Pacific. Tagging results do not contradict either of these systems. Kearney (1978) considered that Fujino's two stocks also differed in the rate of growth of the fish.

Matsumoto (1975) used catch per unit effort data from the longline fishery to suggest patterns of skipjack movement in the Pacific. Positions of high catch per effort per quarter-year were charted and schematically connected in time sequence, on the assumption that the changes in position indicated movements of groups of fish. The charted connections took tagging and other biological information, and surface currents which were assumed to facilitate the movement, into account. This very detailed study suggested the existence of 14 "groups" of skipjack, each characteristic of a large area of the Pacific and moving in a circular pattern in that area during each year. Matsumoto stated that these groups were not necessarily sub-populations, and not

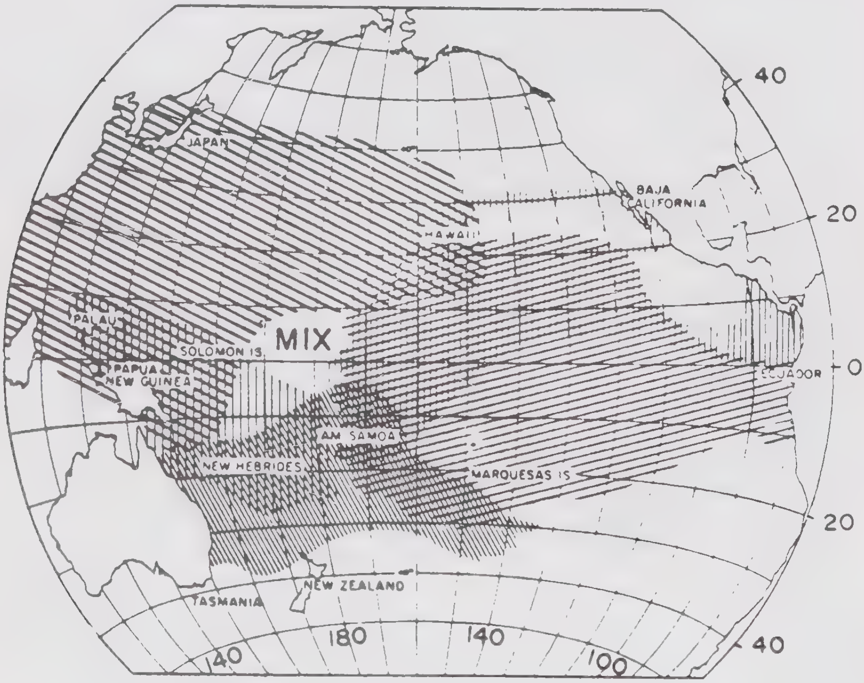

Fig. 7.—The approximate ranges of five populations of skipjack tuna in the Pacific Ocean: from Sharp, 1978.

independent. He noted that the postulated circular movements could be reconciled with zonal and meridional movements known from tagging studies assuming, however, that individuals could transfer between adjacent groups. The need for validation of this scheme of movements was emphasized.

Seckel (1972) considered the migration path to consist of two parts: (1) the distance a fish, or school, is carried by the current, and (2) the distance a fish, or school, swims relative to the moving water or current. He then asked what contribution the current made to skipjack migrating from the eastern to the central Pacific. This was answered by modelling the drift of a floating object under the influence of the geostrophic flow and surface wind drift. Results showed that the time of drift from the eastern Pacific to Hawaiian waters was about the same as that of skipjack tagged in the eastern Pacific and recovered in the Hawaiian fishery. Seckel hypothesized that one of the possible modes of migration for skipjack recovered in Hawaii could be fish randomly swimming in search of food while being carried by the ocean current. Most authors agree that this westward movement from the eastern Pacific is made by young adults in order to reach the central Pacific spawning areas. These fish must originally have moved eastward from the central Pacific, probably as larvae or juveniles, and Williams (1972) suggested three possible modes of movement. All three assumed some kind of active or passive orientation to surface currents, and all are plausible. Field observations are, however, still inadequate to indicate which—if any—of these models is correct.

BIGEYE

Tagging observations on movements of bigeye are very scarce and do not suggest a pattern. The greatest distance travelled by a tagged and recaptured fish is about 1500 km, from west to east as shown in Figure 3 (Kume, 1967; Anonymous, 1979a). No definite information exists about sub-populations. Catch per unit fishing effort varies with season in some areas, but these changes are not well understood (Alverson & Peterson, 1963; Shingu, Tomlinson & Peterson, 1974). Kume (1967) considered that the changes indicate movement from west to east during the life of the fish. There must be considerable meridional movement of bigeye, because spawning areas are known only between 25° N and 15° S (Fig. 11), whereas the species is quite abundant poleward of those latitudes in each hemisphere (Fig. 3). Abundance to the north of 25° N is greater in winter than in summer (Kume, 1967). Nakamura (1969) presented a diagram of distribution and migration which distinguished ontogenetic stages and areas, but not seasons. West-to-east movements of adults were shown in addition to the meridional movements mentioned above. The need for more information, which might lead to a revision of the scheme, was emphasized.

ALBACORE

The northern and southern hemisphere albacore are believed to be distinct stocks or sub-populations. Available data indicate: (1) that albacore do not migrate across the equator in any season; (2) that the areas occupied by the albacore in the two hemispheres are roughly symmetrical (Nakamura, 1969; also see Fig. 4); and (3) that there are separate and distinct spawning grounds and times in the two hemispheres (Fig. 12). The seasons of spawning are in the respective warm (summer) seasons of each hemisphere (Nishikawa, Kikawa, Honma & Ueyanagi, 1978). We concur that there are two distinct hemispheric populations and will discuss them separately.

North Pacific Albacore

Results from tagging studies (Laurs, 1979) suggest that there are at least two sub-stocks of albacore that comprise the North Pacific population, and that these sub-stocks have different migratory patterns. Fish of the northern sub-stock make trans-Pacific migrations between the eastern and western North Pacific, resulting in an exchange of fish between the area of the U.S. surface fishery north of about 40° N and the Japanese surface fishery, and the longline fishery west of 180°. The southern group of fish have a different migration scheme and appear to enter the U.S. fishery south of about 40° N and the longline fishery east of 180°. Only a small proportion of the southern group appear to migrate between the eastern and western Pacific and enter the Japanese surface fishery. During a given season there is also very little exchange of albacore in the U.S. fishery between the northern and southern sub-stocks.

The two surface fisheries, off Japan and North America, are supported by young fish. It still is unknown at which stage of maturity and where, the albacore change their habits and enter the subsurface longline fishery. Hypotheses proposed by Otsu & Uchida (1963) and by Rothschild & Yong (1970) offer different interpretations. The former suggest that the fish move sequentially from the North American fishery through the longline fishery to the Japanese surface fishery, based on the timing of exploitation among these fisheries. On the other hand, the latter authors state that the fish move from the American into the Japanese surface fishery and finally into the longline fishery. They postulated that the fish pass between the peripheral surface fisheries *via* the longline area, but are not vulnerable to the longline gear at those times. The Rothschild & Yong hypothesis is founded upon size distribution, growth rates, and times of fisheries, apparent abundance and some tagging data.

Kikawa, Shiohama, Morita & Kume (1977) and Kikawa (in Anonymous, 1977) hypothesized that four-year old fish migrate from the Japanese surface fishery to the United States surface fishery. Recently, Japanese-tagged fish from the surface fishery in the western North Pacific were all reported to have been recovered during the same season east of their release locations. Some fish were recovered in subsequent seasons to the west of the release sites. Two recoveries have been made off the Columbia River in late September and early October 1974 of fish tagged by Japanese scientists in mid-June 1974 in the Emperor Seamount chain near 34° N: 171° E. General results from western Pacific tagging indicate that albacore move eastward across the Pacific during spring and summer months, and that those from the western side near the Emperor Seamount can migrate to the American fishery area by early fall of the same year (Anonymous, 1978, and Fig. 4).

Western Pacific albacore, taken on longlines in the Philippine Sea in December, are pre-spawners. They move out from there in February and March to the spawning grounds (see Fig. 12). Other pre-spawners occur in the North Pacific Current (see Fig. 8) (winter longline grounds). They may pass through the Philippine Sea or disperse directly from the North Pacific Current to the spawning grounds (Otsu & Uchida, 1963), penetrating a wide area of the Subtropical Convergence (region in which converging currents are present; see Sverdrup, Johnson & Fleming, 1942, p. 140). The latter conclusion is supported by large fish occurring along the southern fringe of the longline grounds in numbers which increase progressively from west to east.

Young albacore of about age 1 year (30 cm) are present in Japanese coastal waters in spring and summer. These are considered to have moved in from the North Equatorial Current spawning ground and to have entered the North Pacific Current area *via* Japanese coastal waters (Nakamura, 1969). One-year olds also occur occasionally in North American coastal waters.

The albacore taken in the North American surface fishery align into three major modal groups at approximately 55, 65, and 75 cm fork length (ages 2, 3, and 4 years, respectively). Fish in the northern portion of the fishery are 2–3 cm smaller at a given mode than those in the southern part (Laurs & Lynn, 1977). These fish all are sexually immature.

Laurs & Lynn (1977) and Anonymous (1977) present evidence for two groups (see p. 456 and Laurs, 1979) taking separate routes of entry into the North American surface fishery. Their interpretation differs from that of Clemens (1961), who postulated a single group which varies in latitude of entry in accordance with variations in environmental factors and travels up

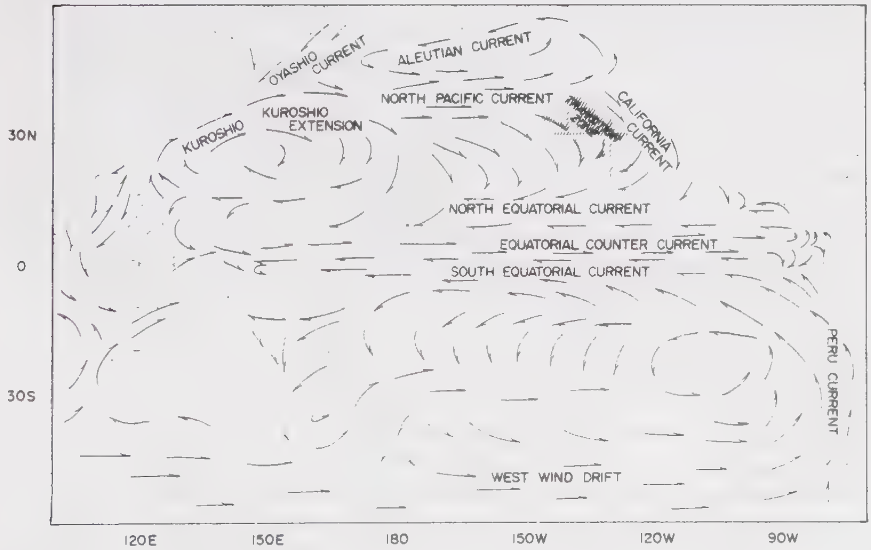

Fig. 8.—Major features of surface circulation: shaded area is the Transition Zone.

the coast as the season progresses. Support for the proposed division of route pattern is found in the length–frequency distribution of the catch. Size compositions recorded during 1972–1974 show different modes in sizes of fish caught off California from those taken off the states to the north (see above). The smaller fish in the northern area presumably convert less energy into growth and more into ocean-wide migration than the fish in the southern area, which are thought not to have moved so far between their passes through the American fishery. Sizes of fish taken offshore from the fishing grounds and south of 35° N indicate that those fish are the ones that move into the southern portion of the fishery. Additional evidence to support this hypothesis has been based on radioactive cobalt fallout data by Krygier & Pearcy (1977). Those investigators also propose one group entering north of 35° N and the other to the south. The division and its location may be modelled in response to the environmental conditions prevailing at the time. Furthermore, Laurs (in Anonymous, 1977) presented evidence that the northern group moves trans-Pacific, while the southern group migrates between the eastern and central Pacific areas. He postulates some degree of intermixing among the two groups.

According to Laurs & Lynn (1977), the general pattern by which the albacore seasonally migrate into the United States surface fishery proceeds in three stages, regardless of which of the two sub-stocks is considered. (1) They migrate eastward from the central North Pacific and form centres of relative abundance within the eastern section of the Transition Zone (Sverdrup *et al.*, 1942, p. 714 and Fig. 8) approximately 1000 to 1600 km off the United States coast in late May and June. (2) They move towards the American coastal regions as nearshore warming occurs; catches during this time indicate that the fish are scattered. (3) By mid-July, concentrations of fish are evident near the coast, often in the vicinity of fronts at the edges of coastal upwellings. Clemens & Craig (1965) reported concentrations of albacore off southern California in June in a number of years.

The eastward migration from offshore central ocean waters to the nearshore area appears to continue throughout the summer. Variation in the migration pattern has been interpreted as responses to variation in surface temperature and other environmental variables (Craig & Graham, 1961; Graham & Craig, 1961; Craig & Caneday, 1962; Craig & Dean, 1968). Laurs & Lynn (1977) concluded that the eastward migration of albacore is linked to the Transition Zone and that variations in the pattern of migration occur in response to variations in the character and development of the Transition Zone and its frontal structure. They believe that when the Transition Zone is narrow and the fronts well defined, the migration is well defined; when weakly developed, the migration is less well defined. The albacore migration is confined to temperatures of about 16° to 19° C; speed of the fish is about 50 km/day for 78–80 cm fish (see also Clemens, 1961); and forage availability is a factor which influences the migratory route. It also is believed that the spring migration is markedly influenced by frontal boundaries and the temperature preference of the fish. Temperature appears to be limiting at the northern boundary of the Transition Zone. At the southern limit of the route, the major limiting factor may be forage availability since this drops off sharply near the southern boundary of the zone. Some foraging is done *en route*, particularly in areas associated with the Transition Zone fronts where the fish may feed for up to several weeks. Since these fish are immature, fat is utilized for migration rather than for reproduction (Sharp & Dotson, 1977).

South Pacific Albacore

Overall, the distributional aspects of the North and South Pacific populations are roughly symmetrical across the Equator. Nakamura (1969) summarized the study of South Pacific albacore made by Kamimura & Honma (1959). Briefly stated, the longline fishing ground is located between 10° and 30° S, and seasonal variations in hook rates are not evident. Segregation of feeding and spawning in the South Pacific is not obvious, although Nakagome (1959) stated that there were southern and northern groups, each of which migrate north in autumn and south in spring; and he assumed the northern group to be spawners and the southern group to be composed of feeding individuals. Various workers have identified oceanographic structures (*e.g.* convergences) which are potentially of ecological significance to the fish (Koto & Hisada, 1967; Yamanaka, 1956).

Taking the minimum size at maturity as being around 90 cm, Ueyanagi (1955, 1957), and Otsu & Hansen (1962) consider those fish in waters north of 30° S latitude to be spawners. The latter authors, however, point out differences in degree of sexual maturity between the fish on either side (north and south) of about 20° S latitude. Size differences noted and indications of a discontinuity structure at that latitude may be evidence of a habitat border in that area (Honma & Kamimura, 1957; H. Nakamura, 1965). Other workers (*e.g.* Hidaka, 1955; Yamanaka, 1956; Koto, 1966; Yamanaka, 1978) indicate a relationship between fish distribution and ocean structure. Zones of fish concentrations are considered to coincide with discontinuities, current rips, and tropical fronts.

Kume & Schaefer (1966) identified separate latitudinal zones occupied by spawners at 15° to 20° S, and by feeding fish at 25° to 32° S. There is evidence of size segregation of albacore in the South Pacific (Saito, 1973) which at times is closely related to ocean structure. The structure of the South Pacific is not as distinct as that in the North Pacific, perhaps because of the less clearly differentiated water masses in the southern ocean.

Not enough information is available to construct a migration model for South Pacific albacore, even though some similarities to the northern pattern are emerging in the New Zealand and Australian areas. An interesting gap in the story is the apparent lack of a habitat corresponding to the one occupied by young fish along the North American coast. There are no surface fisheries of consequence in the South Pacific.

BLUEFIN

Yamanaka & staff (1963) and Bell (1963) reviewed existing knowledge of the distribution and movements of western and eastern North Pacific bluefin, which were then considered as separate species (*Thunnus orientalis* and *T. saliens*, respectively). Later, evidence of trans-Pacific migrations of bluefin in both directions (Orange & Fink, 1963; Flittner, 1966; Clemens & Flittner,

1969) showed that the supposed two species were the same. Much useful information of a general biological nature is also given for bluefin by Bayliff & Calkins (1979) in a paper discussing stock assessment.

On the basis of larval distribution the bluefin appears only to spawn in a single area of the western Pacific, east of Taiwan, although Okiyama (1974, 1979) indicated some isolated spawning in the eastern Sea of Japan in recent years (Fig. 13). Movements of bluefin, after the postlarval stage, are recognized from analysis of fishery statistics, biological information such as length and weight frequencies, and tagging studies. Distribution and movements of the small fish (<20 cm) are unknown but are considered to be gradually northwards in the warm waters of the Kuroshio Current and its branches; however, there may also be some movement southwards as suggested by Bayliff & Calkins (1979). Subsequently, young-of-the-year (zero age class) fish of 20–30 cm (<1 kg) begin to appear off the southern coast of Japan in summer (July); fish in the 2·3–8·3 kg range (age 0+ to 1+) can be found in these same waters during most of the year. These small fish then move northwards with the warm waters of the Tsushima Current into the Sea of Japan, and with the Kuroshio Current into the coastal waters of eastern Japan, where they form the basis for different types of surface fisheries, each with distinct seasonal peaks.

At age 1+, or even younger, most of the fish disappear from Japanese coastal waters although some 2 to 3-year olds are found in the Sea of Japan and off northeast Honshu (Sanriku ground). Many of the small fish migrate into the eastern Pacific where they appear some 12 months later, at lengths of 55–65 cm. Certainly other age classes are involved in the migration, as up to five age classes but usually three (ages 1–3) are represented in the eastern Pacific catch. The bluefin may then leave the American coast after one year or remain for as long as two or three years (as determined by tagging); a small group is found year-round in the neighbourhood of Guadalupe Island, Baja California. Recently, mature fish about 30 kg (age 3+) were reported by Yorita (1976) from fishes caught by set net on the west coast of Hokkaido in July to August, 1972 and 1975. Bluefin appear to re-enter the fishing grounds off Japan (Sea of Japan or east coast) at age three to five years; some are older than this when recaptured, but actual dates of return to these areas are unknown. Relative abundance of fish of age two to five years varies according to the occurrence of dominant year classes. The fish returning from the eastern Pacific join the other immature adults on the Sanriku and Sea of Japan grounds in the summer (tagging data). The age and size of bluefin at first maturity appears still to be in doubt, but is probably 5+ (>140 cm) or older, except in pen-cultured fish (Yamanaka & staff, 1963; Hirota & Masaichi, 1976).

During November and December bluefin off Japan show a general southward movement. By spring (April–June) small and medium size fish (age 4+ to 7) are found on the longline ground immediately to the south of Japan, but not on the more southerly spawning grounds where sexually mature fish (age 6+ to 7+ or older) occur. Subsequently, medium and large fish (immatures and adults) from both these longline grounds move for feeding into the Sea of Japan (mainly caught by set nets and seines) or, more usually, to the Sanriku grounds off northeast Honshu where they are mainly caught by longliners and purse seiners in early summer; they move onto the offshore longline grounds east of Japan in late summer. Bluefin can also be found in waters off Hokkaido and Sakhalin in late summer.

Bell (1963) indicated that commercial production of bluefin off the coast of North America is restricted to the area from 23°–34° N, within 160 km of the coast and usually in the upper 100 m of the water column. Smith & Clemens (1973) stated that the initial approach to land is made in the southerly part of the fishery area, off Baja California, in April–June, with the fish subsequently moving north into southern California waters in July–August as the water temperature increases northwards. Remnants of the population which overwinter in the region are found well to the south in Baja California waters. The occurrence of the bluefin in the eastern Pacific is at much the same time as that of albacore tuna.

Shingu, Warashina & Matsuzaki (1974) reviewed the 1960–1967 longline catches of bluefin in the northern and southern hemispheres from 120° E–160° W. They indicated that, despite the widespread distribution of bluefin, the major longline grounds are near the continents, except east of Japan and near the Equator, where they extend considerable distances eastward. The authors confirmed and strengthened earlier descriptions of the migration routes in the northwest Pacific. Recently, Bayliff and Calkins (1979) presented a model of bluefin migrations which, in addition to North Pacific movements mentioned previously, took into account those bluefin found in the equatorial western Pacific as well as further to the south. The distribution of small surface-caught (by bait boats) bluefin south of 20° N in 1972–1976 suggested that at least some of the fish caught by longline south of the single known spawning ground are the result of larvae, postlarvae, and juveniles moving south from the spawning ground or young fish moving south from Japan.

The western Pacific bluefin fishery is characterized by year classes of varying strength (Yamanaka & staff, 1963; Nakamura, 1969). Prior to 1938 small bluefin were very common off Japan but in the period 1938–1949 were extremely scarce, then again after 1950 became much more abundant as in the pre-1937 era (Yamanaka, 1959; Uda, 1973). Abundance of bluefin in the Sea of Japan fell after 1949 (Uda, 1973). Uda (1957, 1973) has stated that periodic, major changes in the bluefin population off Japan are caused by major oceanographic events such as the abnormal intrusion of cold Oyashio Current water (as in 1941–1945) and subsequent warming periods with a strengthened Kuroshio Current, *i.e.*, when its meandering was reduced (as in 1949–1950). Yamanaka (1978) reported the advent of a strong year class of bluefin tuna a few years after the occurrence of upwelling off the eastern coast of the Philippines. Movements of small fish in Japanese coastal water appear to be related to northward increasing surface temperatures in summer, whilst the larger sized fish offshore appear to stay near the boundaries of cooler water (18–21 °C) or eddies caused by localized upwelling (Uda, 1973). The eastern Pacific bluefin fishery is similarly characterized by varying number and size of the length frequency groups for the years 1951–1978 (Bell, unpubl.; Schultze & Collins, 1977; Anonymous, 1979a), although Bayliff & Calkins (1979) have pointed out the difficulty of assigning ages to length modes. That distribution, movement, and perhaps availability of bluefin is dependent (directly or indirectly) on water temperature is supported by the fact that the fishery was best off southern California in the warm-water years of 1957, 1958, and 1959, and poorest in the cold-water years of 1954, 1955, and 1956. The extensive movements of Pacific bluefin, Atlantic bluefin (Rivas, 1978), and the southern bluefin (see below), all in waters with temperatures from 4°–31 °C, are somewhat similar; each species has localized spawning grounds in the tropics and makes very long zonal migrations of a feeding nature at various developmental stages.

On pp. 460 and 469 it is reported that there is at present only a single known spawning area for the Pacific bluefin tuna (Yabe, Ueyanagi & Watanabe, 1966; Ueyanagi, 1969b; Nishikawa *et al.*, 1978). Little genetic work has been done on the Pacific bluefin except for electrophoretic studies of soluble eye lens proteins from specimens from the California fishery (Smith, 1962, 1966, 1971; Smith & Clemens, 1973) and haemoglobin comparisons by Sharp (1973). Results indicate that the fish show remarkable homogeneity of electrophoretic patterns, even from year to year, and suggest the fish belong to a single North Pacific population exhibiting some local genetic differences on the fishing grounds. Bayliff & Calkins (1979) added, however, that the alternative to a single population might be several sub-populations represented by the various migratory groups: Japan, North America, southwest Pacific. It would be useful to understand this from the point of view of stock assessment.

SOUTHERN BLUEFIN

The distribution and movements of southern bluefin around Australia were reviewed by Robins (1963), whilst Shingu (1967) presented the first comprehensive statement on the species covering most of its geographic range as then known. Subsequently, Hynd (1969), Nakamura (1969), and Shingu (1970) presented rather similar hypotheses of migration routes of southern bluefin, based on commercial fisheries statistics, tagging data, morphometric studies, and oceanographic data. These hypotheses clearly showed the relationship of life history or developmental stages of the species to various oceanographic regimes, including the transition of young surface dwelling fish of coastal waters to the larger immature and adult stages at subsurface levels and the expansion of habitat area with increasing size of the fish.

The species appears only to spawn on the "Oka" ground (Yabe *et al.*, 1966; Ueyanagi, 1969b; Nishikawa *et al.*, 1978; see p. 470 and Fig. 14) in the tropical eastern Indian Ocean south of Java. The movement of the young fish (< 1 year old) is unknown but is probably slowly southwards until they appear in substantial numbers as 1 to 2-year olds in neritic waters of Western Australia. (Ages of southern bluefin have not been determined with certainty.) The hypotheses then indicate movement around into southern and south-eastern Australian waters (excluding Bass Strait) where the catch is mainly of 2+ to 4+-year old juveniles (Robins, 1963; Hynd, Kesteven & Robins, 1966; Hynd, 1969). This largely eastward movement is progressive with time and is accompanied by an increase in average weight of the fish. These fish form the basis of the Australian coastal surface fisheries for southern bluefin in the southern summer off South Australia and in the southern spring off New South Wales. At 4+ years the fish leave the surface fishery for subsurface levels and become subject to longlining. As 5 to 6-year olds they are found further offshore at greater depths and lower temperatures. Distribution of these sub-adults apparently is controlled by seasonal oceanographic conditions. They move northwards to as far as 30° S (in the western Tasman Sea and off the east coast of New Zealand) in winter and southwards (West Wind Drift; see Fig. 8) south of 40° S in warmer months.

By the time maturity is reached at 7 to 8 years old, the fish almost exclusively inhabit the region of the West Wind Drift. The sexually maturing fish (pre-spawners) then migrate to the "Oka" spawning ground through the "Oki" fishing ground west of Australia in the region of 20–30° S: 90–110° E; the returning spent fish also pass through the "Oki" ground. The work of Mimura (1962) and Kikawa (1964) showed that both pre-spawners and spent fish were found on the "Oki" ground from September to April. Gonadal studies by the same authors also confirmed the "Oka" ground as the spawning area from August to March. From the "Oki" ground the spent fish move back to the richer feeding grounds of the West Wind Drift, with some specimens being found on the longline grounds of the Tasman Sea and off New Zealand. The spawning migration (from the West Wind Drift to the "Oka" ground and return) is a meridional movement in what is otherwise a markedly zonal distribution and movement. The authors of the migration models—Hynd, Nakamura, Shingu—and in particular Hynd, showed, from tagging results, the extensive zonal migrations of southern bluefin of at least up to 7200 km, *e.g.* from off South Australia to southeast of Cape Town, South Africa (see Fig. 6). Thus, there is apparently only one stock or population of southern bluefin, with a single tropical spawning area and an immense circumpolar range in temperate waters.

It should be noted, however, that no juvenile southern bluefin tagged in neritic waters (or elsewhere) have yet been recaptured on the "Oka" spawning grounds. An interesting and unusual indirect confirmation of the seasonal meridional spawning movement of adult southern bluefin was provided by Warashina & Hisada (1974), who looked at the temporal and spatial occurrence of "fat" (red meat) and "lean" (brown meat) condition in fish over 130 cm (spawning size). The results showed good agreement with proposed times and routes to and from the "Oka" spawning ground. Hynd (1965) suggested that three separate groups of fish spawn there within the extensive overall spawning season from September to March and all three are later represented in catches of juveniles in Australian coastal waters. Initial surveys of southern bluefin off the Cape of Good Hope (Jager, Nepgen & Wyk, 1963) showed catches were composed of fish about 4 years old or older, suggesting that there was no spawning group in the South African region.

The original hypothesis that all juvenile southern bluefin must migrate through Australian coastal waters was questioned by Hynd (1969), F.A.O. (1975), and Hynd & Lucas (1975). Murphy (1977) has pointed out that Japanese longline catches of 61–80 cm southern bluefin (2¾ to 4 years old) off South Africa are in total as large as, if not larger than, those caught on the longline grounds off Australia. The occurrence in numbers of these sizes of fish simultaneously in both areas suggested that large numbers of juveniles must move from the "Oka" spawning grounds to the longline grounds without passing through Australian neritic waters. Tagging evidence also supports this argument.

Knowledge of the migratory movements of southern bluefin was most helpful in the introduction in 1969–1970 of voluntary restrictions by the Japanese industry of longline fishing effort because of apparent over-fishing of the stocks (Anonymous, 1972; Hayashi [Hayasi], Shingu & Hisada, 1972; Hayashi [Hayasi], 1974; Warashina & Hisada, 1974).

As mentioned, one spawning area ("Oka" ground) is known for the southern bluefin tuna. More than one spawning group may, however, be involved in that area (Hynd, 1965, 1969; Shingu, 1967, 1970). Whether there are any genetic differences in these spawning groups is unknown. Shingu & Warashina (1965) indicated that morphometric studies of southern bluefin from Australia and New Zealand waters showed no separation of stocks. Similarly, blood samples analysed for this purpose at the then U.S. Bureau of Commercial Fisheries Laboratory in Honolulu, Hawaii showed no differences (Hynd, 1969). In fact, tagging studies indicate positive mixing of fish from the Indian and western Pacific Oceans (Hynd, 1969; Murphy, 1977). All these observations indicate that the southern bluefin from all known areas comprise a single stock.

LARVAL DISTRIBUTION, SPAWNING AREAS, AND SEASONS OF TUNAS

Spawning areas of the various tuna species have been defined primarily by capture of larvae and juveniles and by the occurrence of sexually mature adults. The larvae are collected in plankton, nekton, and neuston nets, by dip-netting at the sea surface at night—usually near a light set out for that purpose, and by examination of stomach contents of piscivores (Klawe, 1963). Juvenile tunas have been observed in samples taken by trawls and in the contents of bird and fish stomachs (Higgins, 1970). The occurrence of running ripe adults or adults with high gonad indices (weight of ovaries divided by cube of fish length; see Orange, 1961; Shingu, Tomlinson & Peterson, 1974; Naganuma, 1979 for example) are noted in the course of research or exploratory fishing expeditionary activities and, on occasion, during commercial fishing operations. The vertical distribution of tuna larvae has been examined by comparison of net tows made at the surface with tows made at or through various depth strata. Conclusive evidence is not available, but the consensus of opinion is that the larvae are concentrated above the thermocline, although some have been taken within and below that layer (Matsumoto, 1958; Strasburg, 1960; Klawe, 1963; Ueyanagi, 1969b). There is some evidence that suggests diurnal vertical migration within the upper 50 m (Matsumoto, 1958; Strasburg, 1960). Rarely have enough data been collected to describe definitively any seasonal variation in spawning activity; however, a notable effort in this regard is the atlas derived from Japanese research vessel surveys, 1956–1975, compiled by Nishikawa *et al.* (1978). Their atlas includes charts of the annual and quarterly distributions of the larvae of 14 species of tunas and billfishes and related forms based on about 6000 net tow samplings taken from two research vessels. Another article of major importance is that of Ueyanagi (1969b), which includes some of the same data as in the atlas of Nishikawa *et al.* combined with information from other research vessels. The atlas of Nishikawa *et al.* has a limited areal coverage, especially in the second and third quarters of the year: Ueyanagi summarizes the data into two halves of the year but does not treat them with regard to density of occurrence (Ueyanagi, pers. comm.). Other summary reports of general note are in the Proceedings of the World Scientific Meeting on the Biology of Tunas and Related Species, Vols 1–4, F.A.O. Fisheries, Report No. 6 (Rosa, 1963), and the Proceedings of the Governor's Conference on Central Pacific Fishery Resources, Honolulu, U.S.A. (Manar, 1966).

YELLOWFIN, Figure 9

The warm tropical region centred around the Equator is the area in which yellowfin tuna larvae are abundant. Suzuki, Tomlinson & Honma (1978) identified three high density areas of yellowfin larval abundance (western, central, and eastern Pacific). This was not taken as evidence of the existence of separate stocks or sub-populations but as possible evidence of quasi-independent stocks in the three areas. Periods of spawning in offshore and coastal areas within the eastern tropical Pacific surface fishery area were discussed by Knudsen (1977). Coastal yellowfin of two recruitment groups showed sporadic spawning. In some years there were two peak periods but activity varied from year to year. Offshore fish did not exhibit this variable pattern and spawning periods lasted longer.

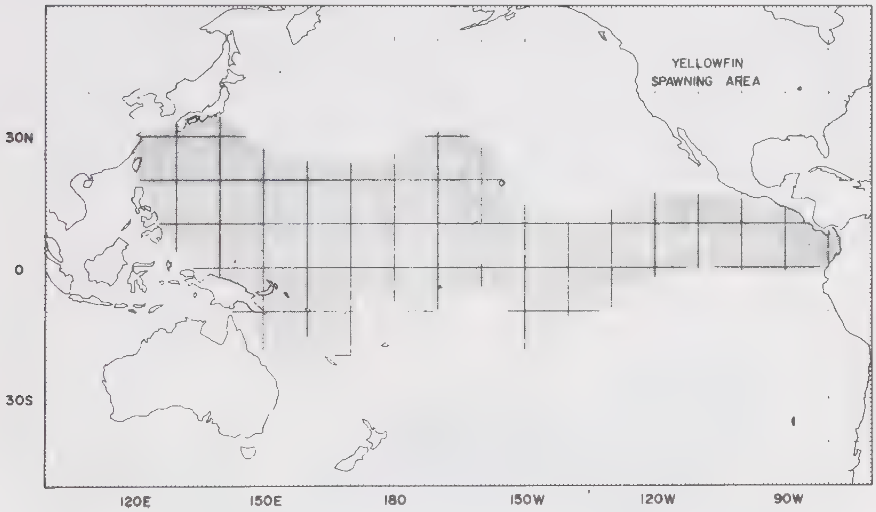

Fig. 9.—Spawning area of yellowfin tuna: shading indicates areal extent of accepted and known spawning ground; this does not necessarily encompass every location from which larvae were collected or sexually mature adults were captured.

Comments regarding seasonal variability of larval occurrence should be taken with some reservation because of time and space limitations of sampling (see above; Ueyanagi, pers. comm.). Throughout this present paper the quarters of the year are: first, January–March; second, April–June; third, July–September; fourth, October–December. During the second quarter yellowfin larvae occur only in the western side of the Pacific between the Equator and 30° N latitude. Spawning is scattered from 130° E to 160° W at 15° N to 35° N and is of low intensity in the third quarter. In the fourth quarter larval occurrences are numerous within 15° north and south of the Equator in the Indo-Pacific with scattered occurrences elsewhere across the entire Pacific within this band of latitude. The first quarter shows some spawning throughout the range from 10° S to about 20° N.

The north–south range in the eastern Pacific around 120° W (0–15° N) is narrower than in the west at 170° E (20° S–25° N), which limitation seems to be in alignment with the temperature field because the isotherms in the east converge towards the Equator from both the north and south. Klawe, Pella & Leet (1970) reported a marked increase in the proportion of net tows containing larvae of yellowfin at stations near the Gulf of California where the surface temperature exceeded 26 or 27 °C. Richards (1969) recorded yellowfin larvae only in waters above 27 °C in the eastern tropical Atlantic.

Collections of larvae taken at the surface and at depths of 20–30 m both conform to the general distribution stated above (Nishikawa *et al.*, 1978).

SKIPJACK, Figure 10

Skipjack tuna larvae have been found over wide areas in all major oceans (Klawe, 1963, 1970, 1972a,b; Nakamura & Matsumoto, 1967; Ueyanagi, 1969b; Mori, 1972; Richards & Klawe, 1972; Chen & Tan, 1973; Matsumoto & Skillman, in prep.). In the western Pacific the known distribution of skipjack larvae extends from about 35° N off Japan to about 35° S off southeastern Australia. The latitudinal range narrows in the central ocean to a band about 15–20° north and south of the Equator; and east of approximately 120° W it is mostly restricted to the strip between the Equator and 10° N. The distribution coincides closely with the area delineated on the north and south by the 24 °C isotherm (Ueyanagi, 1969b).

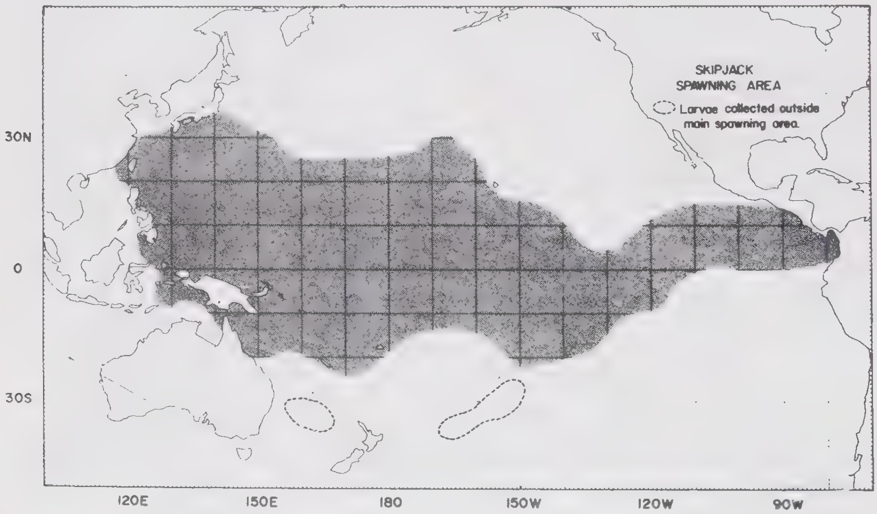

Fig. 10.—Spawning area of skipjack tuna: shading indicates areal extent of accepted and known spawning ground; this does not necessarily encompass every location from which larvae were collected or sexually mature adults were captured.

Spawning activity seems most intense in the western Pacific in the second quarter of the year. The spawning area spreads east and south in the third and fourth quarters, and is diffuse in the first quarter (Nishikawa *et al.*, 1978). Density of larvae increases to the west (Ueyanagi, 1969b).

According to Ueyanagi (1969b) skipjack larvae in the Indo-Pacific are scarce at the surface in daytime, and most were collected in tows in the 20–30 m layer. Night samples showed less variance between the towing depths, but there are still higher numbers of larvae at deeper levels.

Naganuma (1979) consolidated much of the available information on skipjack reproduction in the western Pacific. Spawners range from 40 to 80 cm, occurring widely between 35° N and 24° S. In the North Pacific there is a size segregation in the spawning season such that the larger the fish, the earlier in the year they spawn. Skipjack of 40 to 50 cm size constitute the spawners in the South Pacific. In any area, the spawning that does take place occurs in the warmest season.

It was observed that skipjack larval abundance was highly and positively correlated with high sea surface temperature (Inter-American Tropical Tuna Commission (IATTC), 1973). This led to the hypothesis that warm years in the Central Pacific might lead to higher abundances of adults in the eastern tropical Pacific fishery. Correlation tests indicated that about 50% of the variation in the catch index was attributable to temperature variations although the causal factors are unknown. Attempts have been made to predict abundance about one year in advance based on temperature and atmospheric changes in selected equatorial areas (IATTC, 1973, 1974, 1975). These predictions have, however, often failed (IATTC, 1975). Investigation into the relationships between environmental indices, spawning success and larval survival, and year class abundance in the fishery are continuing.

We wish to point out an apparent contradiction. The spawning and survival of larvae of skipjack apparently is related, positively, to high sea surface temperatures. But physiological studies (see p. 482) suggest that large skipjack—spawners—are adversely affected by high temperatures. Thus, large spawners should not occur in areas in which larvae are found; this, of course, cannot be true. This apparent dilemma can be resolved if the spawning adults occur at depths with cooler temperatures (within the thermocline), if spawning takes place at those depths, and if the eggs float to the surface layer where their survival is enhanced. The young then would be separated from their parents, who are a major predator upon them. On the other hand, there are large adults in Fijian and Tahitian surface fisheries when the surface water is very warm, about 30 °C (Sharp, pers. comm.).

BIGEYE, Figure 11

The entire equatorial region of the Pacific is a spawning ground for bigeye tuna (Kume, 1969). Spawning occurs largely in the warm, low latitude areas on the eastern (0°–10° N) and western (10° S–15° N) sides of the ocean. More larvae have been collected at the surface than at 20–30 m.

Gonad development of adults is at a very high level on the average, with marked seasonal variation in the eastern area. The season of greatest spawning is during the fourth quarter in the equatorial Pacific to the northwest and southeast of New Guinea, in the Hawaiian Islands, and along an equatorial

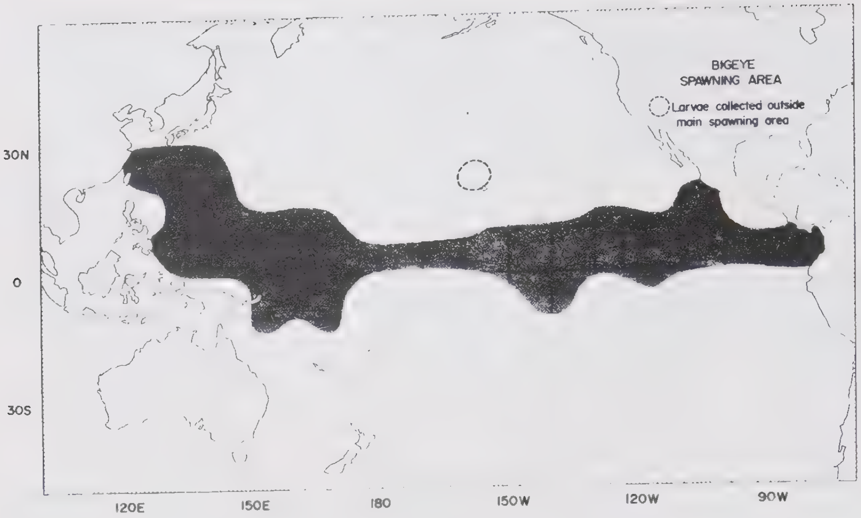

Fig. 11.—Spawning area of bigeye tuna: shading indicates areal extent of accepted and known spawning ground; this does not necessarily encompass every location from which larvae were collected or sexually mature adults were captured.

band extending between Ecuador and about 115° W. There is scattered activity primarily in the western Pacific in other seasons (Nishikawa *et al.*, 1978). Kume (1969) suggested that sexually developed individuals occur in the cooler waters of the eastern part of the range.

Kikawa (1957) reported that the ocean currents in the western Pacific have a definite ecological significance. Bigeye in the North Pacific Current are in a resting stage; those in the North Equatorial Current comprise recruits of the spawning group, and the most mature individuals are dominant in the Equatorial Countercurrent, so that the bigeye spawning area aligns with this current.

ALBACORE, Figure 12

The centres of distribution of albacore larvae are at about 20° N and 15° S; larvae are not found in equatorial waters. The areas of occurrence correspond approximately with the western halves of the subtropical gyres (Ueyanagi, 1969b; Nishikawa *et al.*, 1978). Each range expands meridionally during the warm season and contracts in the cold. Thus, the North and South Pacific spawning areas are assumed to be separate. The spawning grounds are characterized by surface layer (to 50–60 m) temperatures over 24 °C, and no strong thermocline above approximately 250 m (Ueyanagi, 1969b). The possibility of spawning has been reported off Baja California, Mexico, in the vicinity of Guadalupe Island (Clemens, 1961), and fish as small as 30 and 40 cm have been reported in the American coastal fishery (Clemens, pers. comm.; Laurs, pers. comm.).

The peak spawning season in the North Pacific is in summer, broadly

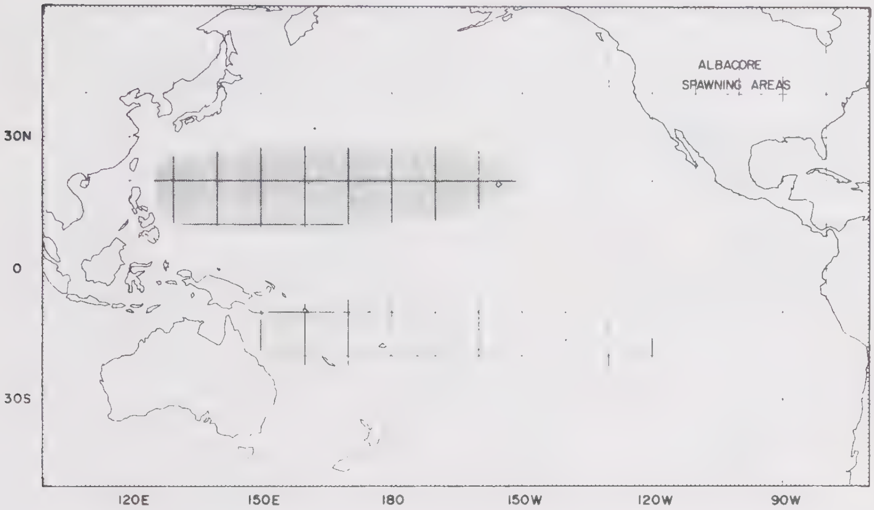

Fig. 12.—Spawning areas of albacore tuna: shading indicates areal extent of accepted and known spawning grounds; these do not necessarily encompass every location from which larvae were collected or sexually mature adults were captured.

speaking, with some activity evident throughout the year in areas south of 20° N. Larval occurrences in daytime net tows at 20–30 m are greater than in tows at the surface, but the tendency is less marked than in some tunas, *e.g.* skipjack (Ueyanagi, 1969b). Numbers taken in night tows at the two levels are similar.

BLUEFIN, Figure 13

According to Nishikawa *et al.* (1978) bluefin spawning occurs only in a limited area off the Asian mainland between 20° and 30° N and extending east to 150° E. The area corresponds to a zone occupied by the Kuroshio Current and the Kuroshio Countercurrent. The known spawning area is rather confined relative to the distributional range (compare Figs 5 and 13) of this species (Yabe *et al.*, 1966). All spawning occurs in April–July. Most larvae were captured at the surface, both during the day and night.

Okiyama (1974) reported the capture of post larval bluefin in waters off Niigata, Japan, and concluded that they were spawned in the Japan Sea. He noted that the ocean conditions at the time (August 1972) were unusually warm and that the occurrence was a rarity. Okiyama (1979) has, however, reported on the occurrence of additional postlarvae off Niigata in August 1974 (14 individuals) and in August 1978 (1 individual). In view of this and previous occurrences, he speculated on the presence of an isolated spawning group of bluefin in the Sea of Japan, which spawns later than the main body of fish to the south, *i.e.*, to the east of Taiwan in April to June. Okiyama commented on this in relation to Kawana's (1935) implication of spawning in the Sea of Japan in years of peak abundance of the species which, of course,

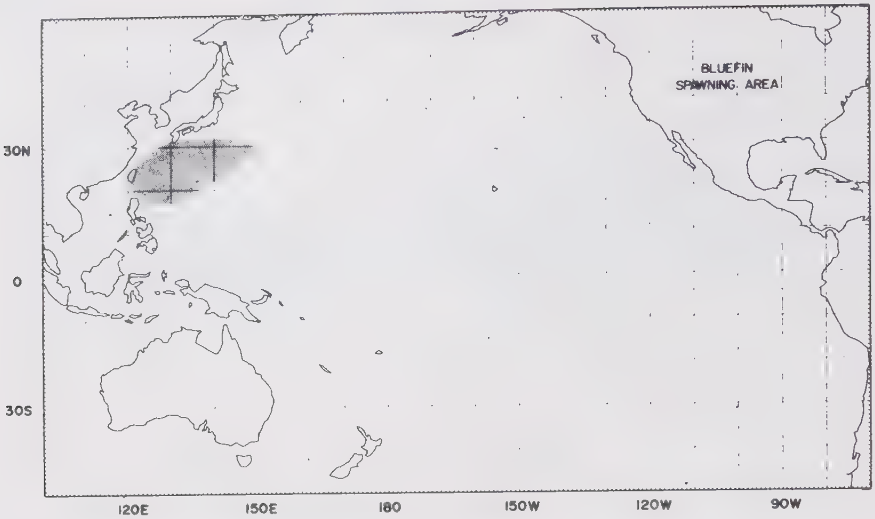

Fig. 13.—Spawning area of bluefin tuna: shading indicates areal extent of the accepted and known spawning ground; this does not necessarily encompass every location from which larvae were collected or sexually mature adults were captured.

may be related to environmental events. Okiyama also reported the appearance of large numbers of juvenile bluefin (zero year class) along the Sea of Japan coast, including Hokkaido, in recent years.

SOUTHERN BLUEFIN, Figure 14

Yabe *et al.* (1966) and Ueyanagi (1969a) found larvae present from October to March. The area of spawning is in a relatively confined part of the eastern Indian Ocean between the Sunda Islands and Australia (Ueyanagi, 1969a,b; Nishikawa *et al.*, 1978). Larvae of southern bluefin are unknown from other oceans. Almost all specimens were collected at or near the surface.

FRIGATE AND BULLET TUNA

Larvae of *Auxis thazard* and *A. rochei* occur largely on the eastern and western sides of the Pacific, extending from 20° S to 30° N on the west and 5° S to 20° N on the east. Some occurrences in mid-ocean have been recorded. In the eastern Pacific most spawning occurs in the fourth and first quarters with no activity in the intermediate period. In the west, most spawning occurs in April to June in the north (20°–30° N) and in October to December in the south and equatorial areas (10°–20° S) (Nishikawa *et al.*, 1978).

LITTLE TUNA

Spawning areas of *Euthynnus affinis* and *E. lineatus* are limited mainly to peripheral areas of the Pacific. Occurrences of larvae are restricted to the

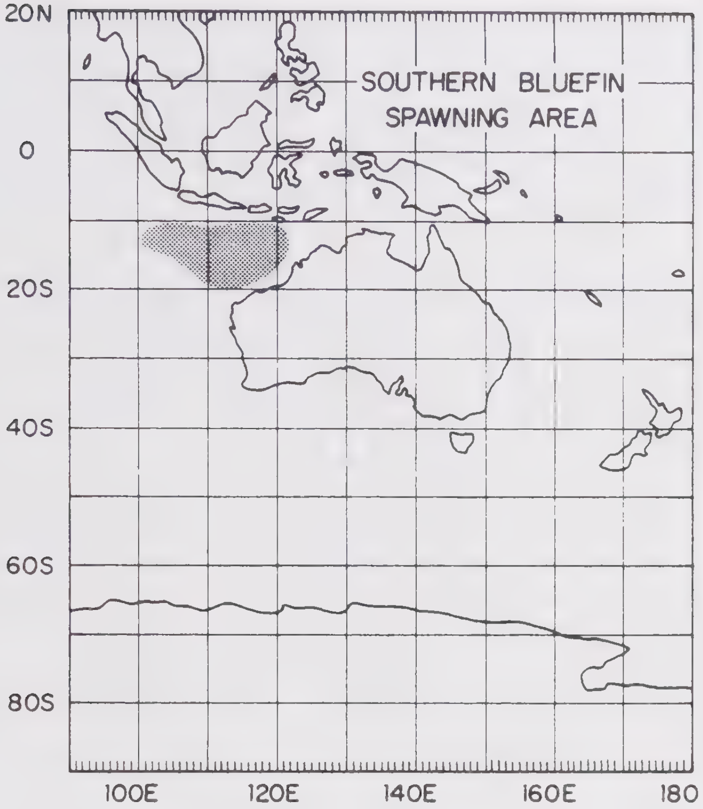

Fig. 14.—Spawning area of southern bluefin tuna: shading indicates areal extent of the accepted and known spawning ground.

first quarter in the eastern tropical Pacific, and to the fourth and first quarters in the western Pacific (Nishikawa *et al.*, 1978).

SLENDER TUNA

The larvae of *Allothunnus fallai*, described by Watanabe, Yukinawa, Nakazawa & Ueyanagi (1966), occur over a wide area of the Indian and South Pacific Ocean in temperate latitudes (20°–30° S). In the South Pacific they were found mostly in November and December, so that spawning is assumed to be a late southern spring event. The area of spawning is in southern waters slightly colder than, but contiguous with, those of the albacore. Of all the tunas, the slender tuna appears to spawn in the coldest waters.

INDO-PACIFIC DOGTOOTH TUNA

All recent collections of larvae and juveniles of *Gymosarda unicolor* were made in the tropical and subtropical western Pacific. An advanced larva was identified in the "Dana" collection from the easternmost Indian Ocean.

Collections range over a wide area of the tropical and subtropical western Pacific, from approximately 10° N to 20° S. Concentrations occur near the shallow seas along island clusters such as the Carolines, Solomons, and New Hebrides. All specimens were taken at the surface and subsurface to 20–30 m, with higher numbers in the deeper net hauls. There is evidence of vertical diurnal migration by at least the advanced larvae. Water temperatures at the collection sites were around 27 °C, or higher. The data indicate spawning activity throughout most of the year (Okiyama & Ueyanagi, 1977).

INFLUENCE OF THE OCEAN ENVIRONMENT ON LARVAE

The major and most obvious influences exerted by the ocean on larvae are: (1) provision of conditions suitable for spawning and subsequent survival of larvae, and (2) drift or transport of larvae to areas with beneficial conditions of adequate food and physical well being.

We have seen that two primary types of spawning activity exist: (1) broad activity (*e.g.*, yellowfin, skipjack, bigeye) over extensive areas and times, and (2) activity confined to specific areas and times. The latter type is particularly remarkable because it is exhibited by the most migratory species such as bluefin and southern bluefin. The evolutionary trends in the physiology of these species have allowed penetration into cooler temperate ocean areas, but the requirement for spawning in warmer tropical waters has remained. The detailed mechanisms by which adults of these latter species navigate extensive distances to the relatively small areas in which they spawn, remain unknown, although there apparently is some form of genetic imprintation.

A series of related questions pertain to whether the fish are "active" ("directed") in their migrations or movements or whether "passive" or random movements can account for them. A combination of "active" and "passive" situations (Williams, 1972) is, of course, possible which could account for changes in behaviour with age, physiological state, *etc*. Furthermore, the environmental stimuli to which the fish respond in these behaviours are almost totally undefined (see p. 452), although one might speculate that they may be related to cyclical endocrine changes (Williams, 1972, 1976). Models such as Seckel's (1972) skipjack drift hypothesis account for at least major portions of the time–place movements, but do not explain such events as repetitive return of adults to limited spawning areas within limited time frames.

RÔLE OF TEMPERATURE IN TUNA SPAWNING ACTIVITY

Numerous authors cited elsewhere in this review have stated that temperature is in some way related to the distribution of adults and to the spawning of tunas and survival of the larvae. The analyses concerning larvae, however, have often been superficial and the relationships break down when it is attempted to apply them over wide areas or extensive times (*e.g.*, IATTC, 1973, 1974, 1975). Klawe *et al.* (1970) concluded that there is little, if any, influence of surface temperature, surface salinity, and seasons on the distribution and abundance of most larval tunas. Temperature, however, was shown clearly to be an important variable for *Auxis* sp., a curvilinear relationship being demonstrated, with optimum temperature near 27 °C.

The authors found a marked increase in the proportion of net tows containing larval *Thunnus albacares* and *Euthynnus lineatus* at stations where surface water temperatures exceeded 26 or 27 °C. As noted below temperatures of 26 °C or higher seem to be required for hatching of yellowfin larvae in captivity.

No other environmental variable has been conclusively shown to influence spawning or larval survival. Data on the water quality or conditions in experiments and culture operations wherein tunas have been reared are given below. Hydrographic data on the physical and chemical properties of water observed quasi-synoptically with larva collections have not been successfully evaluated regarding any meaningful relationships. The lack of any relationship between zooplankton and capture of larval *Auxis* sp. has been documented by Strasburg (1960), Nakamura & Matsumoto (1967), and Klawe *et al.* (1970). Salinity likewise proved ineffective in explaining variations in *Auxis* catches, and it was suggested that the range of salinity values of the waters encountered are unimportant in affecting its distribution.

OCEANOGRAPHY AND THE CULTURE OF TUNAS

Since 1970 there has been considerable effort in Japan devoted to the culture of tunas (Ueyanagi, 1978). The coordinated Japanese plan had two objects which formed the basis for two research projects: (1) to develop rearing techniques for larvae and juveniles resulting from artificially fertilized eggs, and (2) to develop rearing techniques for young tunas caught at sea. The projects have been described in some detail by Ueyanagi (1978 and references therein) and Anonymous (1973, 1979b). The matter of interest for our purposes is the environmental conditions which were found to be suitable or unsuitable for the fish.

With regard to the first project (culture *per se*), comment is limited here to aspects with ecological–oceanographic implications (for discussion of technical details of rearing see original publications). Yellowfin tuna was the target species for experiments from 1970–1976 and artificially fertilized eggs were hatched and the larvae grew to 4 cm length in 28 days. Maximum survival was 38 days, by which time the remaining larva had reached the juvenile stage and was 5·1 cm and weighed 1·35 g. Successful hatching was achieved in the temperature range 26–30 °C. Ueyanagi (1978) considered that the major impact of the work was (1) verification of the identification of yellowfin larvae made by other means and (2) confirmation that yellowfin spawning grounds may be delineated by the 26–30 °C isotherms and that 26 °C is probably the lower limiting temperature for spawning. Much of the success with the yellowfin was considered to be due to the earlier rearing and larval feeding work carried out with the frigate tunas, *A. thazard* and *A. rochei*, and the bonito, *Sarda orientalis*. Ueyanagi stressed the importance of the right type (quality) and size of food for the yellowfin larvae at critical developmental stages, *i.e.*, 7 mm, 10 mm. The high mortality of tuna larvae in nature presumably occurs at times when there is a change in food preference and hence relates to the density of available, suitable food organisms during these critical periods.

In the second research project, the target species was the bluefin tuna. Young bluefin of 0·25–2·0 kg, caught in set nets and by trolling, were reared in floating pens (similar to those used for the yellowtail, *Seriola quinqueradiata*) in sheltered coastal waters, mainly in southern Japan. Considerable mortality was caused initially by the capture, transportation, and transfer of the fish to the pens, and also by the abrasive action of the pen walls on the fish. It is important, however, to consider the causes of mortality other than those mechanical ones for which remedies are being developed. The most important of the environmental conditions affecting the bluefin appeared to be heavy rainfall, which caused rapid lowering of salinities; high levels of sedimentation and pollution, either directly from the land or from river run-off (free swimming tunas might be expected to avoid or leave such areas); and the increase in light intensity following changes in netting in the pens. The disadvantages of locating the rearing pens in coastal waters were off-set by the plentiful supply of natural food in such sheltered areas, good water exchange, and ease of logistical support for the facilities.

After acclimatization, the daily feeding rate of young bluefin was about 10% of body weight during periods of high water temperature. The rate decreased rapidly with decreasing water temperature to about 3% of body weight in mid-winter. Bluefin tuna grown in pens showed that they could survive winter water temperatures down to 12 °C but, as reported by Hirota & Masiachi (1976), growth (and survival) the following year was normal only if the winter temperatures were 15 °C or above. Initial experiments showed growth of bluefin cultured in pens was rapid, from 0·25 to 0·30 kg in mid-August to 2·5 to 3·0 kg in December, a ten-fold increase in just four months. After the winter in which growth was nil, growth re-started in April of the following year. In later successful long-term experiments, bluefin showed growth from 0·14 kg in July-August 1972 to 4·5 kg in March 1973; to 15–17 kg in March 1974; to about 30 kg in March 1975; and to 50 kg in October 1975. Recently, Anonymous (1979b) has reported that Dr Harada and his group at Kinki University had achieved the first successful artificial fertilization and hatching (June 1979) of bluefin tuna eggs spawned naturally by pen-raised fish which were then 5 years old at about 100 kg and 1·9 m in length. Temperature was held at 22–24 °C in the well-oxygenated water in the hatchery tanks; larvae were fed *Chlorella* and grew 4 mm in 4 days.

There is only fragmentary information on pen culture of other tunas. In the dogtooth tuna, *Gymnosarda unicolor*, feeding and growth were normal at temperatures of 18 °C and above, but feeding stopped at 16 °C and death occurred at 14 °C. On the other hand, the bonito, *Sarda orientalis*, survived winter water temperatures as low as 14 °C and exhibited no subsequent growth problems. In 1978 Harada and his group were able to rear bonito larvae from fertilized eggs collected from fish grown in holding pens.

PHYSIOLOGY AND BEHAVIOUR IN RELATION TO TUNA HABITAT

It is only in the last few years that it has become possible to specify some of the habitats of tunas from experimental data, instead of relying entirely upon comparison of distributions of tunas from catch data and environmental variables observed at sea. Much of the experimental work has been done in Hawaii, and owes much to early encouragement by A. L. Tester and later directors of the Honolulu laboratory of the National Marine Fisheries Service. The 1960s saw the perfecting of techniques for handling and holding small tunas at the Service's Kewalo Research Facility at Honolulu (Nakamura, 1960, 1962, 1964, 1966, 1972; Magnuson, 1965). Many of the studies of sensory and auditory physiology, chemoreception, general physiology, and behaviour which took place in the 1960s and early 1970s (Dizon & Sharp, 1978) were directed at understanding responses to fishing gear and improving harvesting techniques. These gave rise to more sophisticated experimental and theoretical studies in physiology, biochemistry, and hydrodynamics, dating from the mid-1970s to the present, which were reviewed in detail by Sharp & Dizon (1978), Magnuson (1978), Stevens & Neill (1978), and Dizon & Brill (1979). More attention has been paid to skipjack than any other species.

Studies of the physiological ecology of tunas have progressed to the point where possible evolutionary trends can be related to distribution in the ocean. Sharp & Pirages (1978) compared morphological characteristics such as distribution of red muscle, development of cutaneous vasculature, and development of central vasculature and associated retia, together with biochemical characteristics such as electrophoretic mobility of proteins, in several species of scombroids. They suggested that these characteristics indicate the temporal order of events in the colonization of habitats in the oceans. Earlier, Sharp & Francis (1976) showed that, based on energy expenditure and growth energetic studies of exploited stocks of yellowfin in the eastern tropical Pacific, morphological and physiological characteristics changed considerably with life history stage and that these related to their oceanic distribution. The two muscle types (red and white) and the vasculature are especially adapted to the respiratory and energetic requirements of tunas with different habits and habitats. In particular, the internalization of red muscle is found in the larger tunas which are widely distributed in the oceans, and has progressed farthest in the species which have extended into temperate waters—albacore and especially bluefin and southern bluefin. Sharp and Pirages concluded that tunas were originally inshore tropical fishes (as some still are) which through biochemical and morphological adaptations extended their ranges, made themselves less dependent upon environmental fluctuations, and reduced their competition. The extreme case is that of albacore, bluefin, and southern bluefin which spread to temperate ocean waters and make long migrations there. Yellowfin and skipjack are intermediate between the temperate and the coastal-tropical tunas (*e.g. Euthynnus affinis*) of today. Yellowfin and skipjack are warm-water cosmopolitan forms with complex population structure which do not make such long migrations as the temperate species. That the tunas indeed had a tropical origin is confirmed by the apparent need of their larvae for very warm conditions (see pp. 464–473).

One of the most interesting features of tunas is that they cannot be strictly classified as either poikilotherms or homeotherms and, unlike other teleosts, are "thermoconserving" fishes (Dizon & Brill, 1979), meaning that they maintain muscle temperatures above ambient. Sharp & Vlymen (1978) tabulated observations by various authors on the differences between tuna body temperatures and ambient temperatures and these ranged from 1–21 °C. Stevens & Neill (1978) have reviewed in detail the thermo-conserving mechanism, which is the countercurrent rete (heat exchanger) of the vascular system to the trunk musculature in the true tunas (tribe Thunnini), first pointed out by Kishinouye (1923).

There has been considerable discussion regarding whether or not tunas can regulate their body temperature, with particular reference to the skipjack (Dizon, Brill & Yuen, 1978; Stevens & Neill, 1978) and the Atlantic bluefin (Carey & Teal, 1969; Carey & Lawson, 1973; Neill & Stevens, 1974; Stevens & Neill, 1978). More recently, Dizon & Brill (1979) have presented an excellent detailed account of thermoregulation in tunas. They considered that the thermoregulatory options of tunas are: (A) behavioural thermoregulation represented by (i) environmental (habitat) selection and (ii) control of activity-dependent heat production; (B) passive thermoregulation (which stabilizes muscle temperature and requires no central nervous system (CNS) intervention) represented by (i) water temperature-related and swimming speed-related heat production, (ii) thermal inertia, and (iii) swim velocity-related heat dissipation; (C) physiological thermoregulation (requiring ability of the CNS to alter the effectiveness of thermo-conserving mechanisms). Dizon & Brill (1979), based on their analysis of previous work and their own experimental observations, concluded that tunas are capable of some degree of physiological thermoregulation, in addition to behavioural and passive thermoregulation. Physiological thermoregulation mechanisms are indicated by the labile and independent nature of excess muscle temperatures with respect to swimming speed and hence heat production. In addition, high speed swimming requires mechanisms to dissipate rather than concentrate the almost cubic increase in heat production. The physiological processes which could serve to adjust heat dissipation rates per degree of driving gradient are alterations in (i) circulatory patterns to change the effectiveness of the heat exchangers and (ii) the relative contribution of the red and white muscle fibre systems to propulsion.

Several authors, such as Dizon *et al.* (1978), have emphasized the advantages to tunas of warm body temperatures and large thermal inertia. Brill's (1978) experiments with skipjack white muscle showed that elevated muscle temperatures are related to increased swimming speed, but he did not know which caused which. Similarly, Bone (1978) suggested that the advantage of high muscle temperature lies in the greater power available from a given muscle mass rather than in the possibility of operating at more or less constant muscle temperature in waters of differing ambient temperature. Stevens & Neill (1978) pointed out that after severe exercise, warmth (high body temperature) is of adaptive value, promoting rapid recovery and thus permitting more frequent feeding frenzies. Recently, Dizon & Brill (1979), Guppy, Hulbert & Hochachka (1979) and Hulbert, Guppy, Murphy & Hochachka (1979) and references therein have indicated that tuna white muscle fibres can function at speeds only slightly above basal rates. Because much of the blood supply of the white muscle by-passes the heat exchangers, aerobically generated heat is not retained and is dissipated at the gills and skin in the usual teleost fashion.

Neill, Chang & Dizon (1976) thought the value of thermal inertia would lie in making tunas relatively independent of changes in water temperature encountered when moving between the upper mixed layer and the thermocline. Graham & Diener (1978) agreed, citing observations on skipjack and *Euthynnus*. Skipjack are oceanic and may penetrate into cooler waters of thermoclines as deep as 200 m (Fig. 15) on a more regular basis than the more coastal *Euthynnus* spp. during foraging and in escaping from predators. The larger and more efficient heat exchangers in the skipjack enable it to go deeper and stay there longer, because reduced heat loss and large thermal inertia prevents the adverse effects from rapid changes in ambient temperature at the thermocline. Thermal inertia may also permit or enhance detection of weak temperature gradients in the sea (Neill *et al.*, 1976). Core temperature changes slowly, so that differences between core and ambient temperature could increase to the point where they are detectable by the fish. Such a mechanism might explain some observed relations between tuna distribution and weak horizontal temperature gradients. Perception would be of the same order as open ocean gradients: 0·0001° to 0·001 °C/m (Stevens & Neill, 1978).

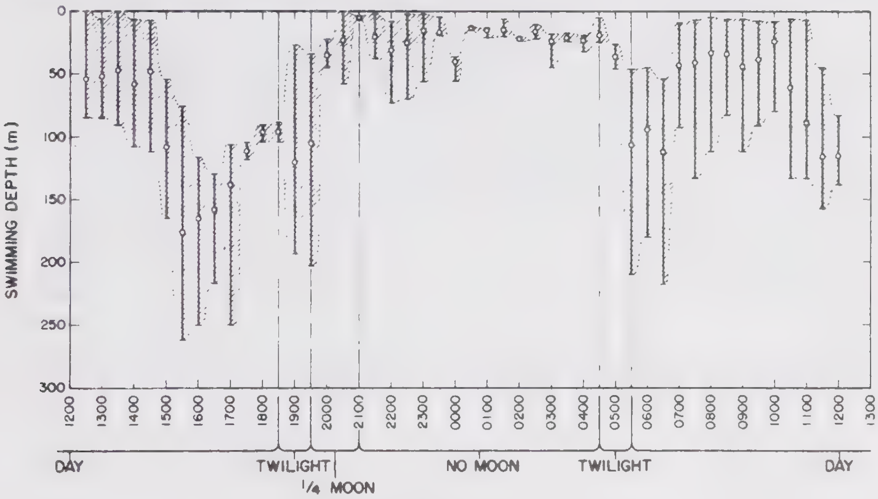

Fig. 15.—Swimming depths of skipjack tuna near Hawaii marked with sonic tags: after Dizon, Brill & Yuen, 1978.

The effects of variations in important ocean properties (temperature, salinity, and dissolved oxygen) have been determined experimentally, mainly for small skipjack, yellowfin, and kawakawa (*Euthynnus affinis*). Dizon, Neill & Magnuson (1977) found that, for skipjack (30–60 cm) and kawakawa (44–50 cm), the lower and upper lethal temperatures were 15 and 33 °C, respectively. All fish stopped feeding within 1 to 2° of the lethal limits. The same work, and that of Stevens & Fry (1971), showed no increase in swimming speed of those species with increase in ambient temperature. Dizon *et al.* (1978), however, in an extensive series of experiments with skipjack, noted slightly higher swimming speeds at higher temperatures. Behavioural responses were also noted in skipjack when tank water was cooled to 20 °C; the fish began to show stress reactions or would not enter the cool water. This work by Dizon *et al.* supported the results of field observations on tracked tagged skipjack by the same authors and by Yuen (1970).

Dizon (1977) showed experimentally that young skipjack and yellowfin exhibit no response to alterations in salinity between 34 and 29‰. Hence, the relatively small salinity changes encountered in the ocean by those and other species are unlikely to regulate their behaviour or habitat. On the other hand, behavioural responses to low oxygen levels were dramatic in experiments on small skipjack (Dizon, 1977; Gooding & Neill, in prep.). An initial reduction from oxygen saturation levels to 2·8 ml/l produced no change in swimming speed or survival time. Below that level swimming speed and mortality increased rapidly at successively lower oxygen concentrations. Only three out of eight skipjack survived at 1·8 ml/l, even for short periods. The increase in swimming speed seems not to be for increase in ram jet ventilation, and is probably an escape response to an unfavourable habitat. Other experiments indicated that oxygen levels as low as 1·4 ml/l were tolerated by yellowfin without signs of stress (Dizon, 1977), and by kawakawa for short periods when searching for food. We discuss on pp. 481–487 the conclusions that authors have drawn from these experiments at different levels of temperature, salinity and dissolved oxygen, regarding the areal and vertical extent of suitable habitat for tunas in the Pacific.

Neill *et al.* (1976) showed from observations on captive skipjack that the thermal inertia is dependent upon fish weight, so that large skipjack would overheat in warm waters if they were as active as small skipjack. It should be pointed out, however, that the value of basing future work on body temperature-limited activity in skipjack has been questioned by Dizon & Brill (1979). Dizon & Brill 'force-swam' skipjack in 30 °C water and observed that excess body temperatures actually decreased or remained constant even though heat production was markedly increased. Assuming that the highest observed muscle temperatures (35 °C) are the highest at which the fish can live, Neill *et al.* (1976) used their data to estimate upper limits of environmental temperature at a normal level of activity. Examples are mentioned on pp. 482–485. Kitchell, Neill, Dizon & Magnuson (1978) suggested that energetic limitations vary according to body weight in skipjack and yellowfin. Growth in fish less than 7 to 10 kg appears limited by food availability, but the growth in fish weighing more than 7 to 10 kg is probably limited by their ability to consume and process available food. The risk of overheating core tissue may restrict activity, and thus the amount of food that can be gathered, in skipjack at the observed maximum weight of 22 to 25 kg. For a variety of reasons the authors have less confidence in explaining the much greater maximum weight of yellowfin (about 182 kg) in the same way.

Sharp & Dizon (1978) have pointed out the results of the deviation of the tunas from the biochemical and respiratory norm of the teleosts. First, these adaptations in tunas result in the high speed, continuous swimming behaviour (Magnuson, 1970, 1973, 1978) necessitated by lack of, or reduction in, the swim bladder (at least in specimens less than 60 kg) and resultant drag, as well as the need for continuous passage of large volumes of water over the gills. Magnuson (1978) indicates that in an evolutionary sense these changes probably took place to permit increased vertical mobility, especially near the sea surface, which is important for food capture and escape from predators. A new hypothesis advanced by Magnuson is that the negative buoyancy (causing the need for continuous swimming) makes possible gliding and soaring in internal waves near the surface of the thermocline. Under these conditions, horizontal motion in the sea would be nearly effortless under certain circumstances. At this time, however, there is little evidence in support of this idea. Secondly, the adaptations in tunas account for the bulk of caloric expenditure, and hence their high daily food requirements (Sharp & Francis, 1976).

Some of the experimental and field work on the limits of tuna habitat imposed by temperature and oxygen has application also to the tuna's vulnerability to fishing gear in different regions, although few published studies are available. Vertical thermal structure is important to longline fishing success, which is less directed as to species than is surface gear. Longline catches are typically multi-species, whereas surface catches are of only one or two species. Using vertical longlines, Saito (1973) and Saito & Sasaki (1974) demonstrated distinct vertical stratification of tunas, as well as high availability, at depths much greater than those normally fished. That lower oxygen tolerances are of considerable potential importance to longline fishing was illustrated by Hanamoto's (1975) work. He showed a decrease in catch success for bigeye tuna when the oxygen concentration at 100 m was less than 1 ml/l. Similarly, where bigeye and albacore distributions overlapped, the albacore catch declined before bigeye presumably because of the lower oxygen values, even when temperatures were satisfactory for albacore. In the eastern Pacific yellowfin fishery Green (1967) demonstrated a significantly greater success of capture by purse-seine net where the thermocline was shallow (less than 20 m below surface) and the mean vertical thermal gradient sharp (greater than 0·55 °C/m). The effects of these two features were additive. The interpretation was that the yellowfin would have to descend into unsuitably cold water in order to escape under the net before it was pursed. Green believed that the vertical distribution of dissolved oxygen also affected the success of purse-seining in the same way, but he gave no data. This work was extended by Sharp (1978) who analysed data on catches from successful purse-seine sets as a function of time of day, depth of the mixed layer, and depth of the 23 and 15 °C isotherms over a period of six months. The work showed (at least for 1973–1974) that the productive area of the purse-seine fishery for yellowfin in the Pacific could be described exclusively as the area where the 23 °C isotherm is less than 50 m below the surface, and the 15 °C isotherm no deeper than 80 m below surface. Based on the criteria mentioned above, Sharp presented charts for each month showing areas where yellowfin are expected to be most vulnerable to purse-seining. He emphasized that his criteria would not predict occurrence of yellowfin or fishing success in optimal habitat areas.

Sharp (1978) attempted a similar treatment for skipjack in the Pacific, with a series of monthly charts showing areas of presumed highest skipjack vulnerability to surface fishing. The areas were based upon the depth of the 15 °C isotherm, the surface temperature, and the depth of the 2·5 ml/l value of dissolved oxygen. The central Pacific provides the most suitable habitat for skipjack which probably is the reason why the species spawns there with movement to the more productive, peripheral areas of the ocean for feeding and subsequent maturation of the gonads. There are, however, at least five genetic units of skipjack in the Pacific which overlap geographically to varying extents (Fig. 7); and Sharp (1978) cautions the extrapolation of data from specimens of one sub-population to the others because of the difference which might be expected in physiology and behaviour. He points out that, in the genetic sense, morphological and biochemical patterns have a probable rôle in the skipjack coping successfully with the diverse environments of the differing Pacific geographic regions. Physical factors, such as high ambient temperature, are very important to rapid growth and development. In areas with very high sea temperatures (greater than 28 C) over most of the year, migration activity can be expected to be slight because of the high respiratory rate needed in warm water. This probably accounts for the reported slow rate of growth of skipjack in the Papua–New Guinea region. Behaviour is probably similarly determined, as shown by the data in Table I on schooling activities in various areas of the Pacific.

TABLE I

Data on schooling activities of skipjack in different areas of the Pacific Ocean (after Sharp, 1978, Table VII)

Exploited group	Average school size (tons)	Bait fishing method	Mixed layer depth in fishing areas	Optimum temperature range of commercial activity
Northeastern Pacific	5–25	stop schools with bait	30–100 m	20–26 °C
Southeastern Pacific	1–25	walking schools	20–100 m	20–28 °C
New Zealand	10–30	stop schools with bait	20–90 m	17–23 °C
Papua New Guinea, Solomon Is.	10–15 (?)	drift into schools	100–300 m	28–30 °C
Northwestern Pacific	3–10	walking schools	50–200 m	20–28 °C (?)

In a relative sense, smaller schools of skipjack tuna are found in areas where the mixed layer is very deep compared with those from areas with more compressed mixed layers. In the latter situations there will be more schools in a smaller volume, hence they will be more likely to aggregate; this also leads to heterogeneity in the population.

TUNA DISTRIBUTIONS IN RELATION TO THE ENVIRONMENT

TEMPERATURE

Blackburn (1965) considered that the following temperatures directly limit the range of adult yellowfin areally and bathymetrically: 18 to 31 C for all occurrences and 20 to 30°C for occurrences in abundance. Two references to occurrence at 15°C, including one for surface fish, were omitted (Bini, 1952; Uda, 1957). The principal evidence of temperature-limitation was that the range of surface yellowfin expands and contracts at its periphery in the same way as the area in the stated isotherm range at the sea surface, in areas with good time series of data (Blackburn & associates, 1962; Broadhead & Barrett, 1964). Such data were not available for subsurface fish, for which depth of capture was not precisely known. Blackburn (1965) assumed a mean capture depth of 100 m (see p. 451) and noted that temperatures there were generally not below 20 °C in areas where yellowfin were taken in abundance.

Subsequent surface observations confirmed the congruence of yellowfin areas and areas over 20 °C off Baja California (a fringe area for yellowfin), except for one situation when the fish occurred at 17 °C. On that occasion 17 °C was the highest temperature at which yellowfin could find abundant food in the area (Blackburn, 1969a).

Bathymetric data on yellowfin were summarized earlier (see p. 451). Yellowfin occur as deep as 380 m. They may even occur deeper, since 380 m was the maximum fishing depth, but the numbers taken declined below 300 m. This work was done west of Fiji, where the mean temperature at 400 m is 13 to 14 °C (Muromtsev, 1958). In a comparison of mean yellowfin catches using the regular longline, fishing to about 130 m, and of another type that fished to about 260 m, the ratio, deep/regular, was 0·73. From this and other information it was concluded that subsurface yellowfin are generally above the thermocline, as hypothesized earlier by Suda & Schaefer (1965), although the above-mentioned findings at Fiji indicate some occurrence in the thermocline as well. In the eastern tropical Pacific, a sharp oxycline accompanies the thermocline. This would further tend to limit the depth range of tunas in that area, as is mentioned later. Temperatures at the top of the thermocline are almost always over 20 °C in the areas where yellowfin are taken most abundantly by longline, which are mostly very near the Equator (Robinson, 1976; Suzuki *et al.*, 1978). The equatorial mixed layer is generally thicker than 100 m in the western Pacific but much thinner, frequently less than 30 m, in the eastern Pacific (Robinson, 1976; Wyrtki, 1964). Thus, if mean hook depth for the regular longline is 100 m, most hooks would hang in waters much colder than 20 °C in the eastern equatorial Pacific. Then if temperatures below 20 °C are unsuitable, longline fishing for yellowfin should be much less successful in the east than in the west, which is the case (Suzuki *et al.*, 1978). Surface yellowfin, however, are more abundant, or at least more vulnerable to capture, in the east (see p. 446 and p. 448). The elevated thermocline may concentrate them near the surface. Small yellowfin (40–70 cm) are found at current boundaries where the sea surface temperature is greater than 23 °C but rarely below that level. This is because they are more sensitive than are large yellowfin (greater than 70 cm) to colder than optimal water, and because of the greater thermal inertia in large specimens (Neill & Stevens, 1974).

Thus the previous hypothesis that the range of yellowfin in abundance is directly limited by a water temperature about 20 °C, both in the horizontal and vertical planes, remains plausible. The species occurs occasionally in deep waters as cold as 14 °C, however, and in surface waters as cold as 15 °C. The large subsurface yellowfin may tolerate slightly lower temperatures than the smaller surface fish.

There is general agreement that certain temperatures likewise limit horizontal and vertical distributions of skipjack, but these temperatures can vary by region and by size of fish. Limits of surface range of skipjack in the eastern Pacific have been compared with contemporaneous surface temperatures by several authors. The limiting temperatures are about 17 to 30 °C for all occurrences and 20 to 29 °C for occurrences in abundance (Broadhead &

Barrett, 1964; Blackburn, 1965, 1969a; Williams, 1970). In Japanese waters, skipjack occur between 18 and 30 °C (Uda, 1957). Off eastern Australia, however, the lower temperature limit for all occurrences is 15 °C, and the upper limit may also be lower than in the eastern Pacific and Japan (Robins, 1952; Blackburn & Serventy, in press). This may represent a difference between sub-populations. Skipjack was seen at 185 m (temp. not < 17 °C; Anonymous, 1965) and a sonically tagged one was tracked at 200 m (temp. 12–14 °C but little time spent at < 18–20 °C; Dizon *et al.*, 1978); both cases were off Hawaii.

Captive skipjack in Hawaii were subjected to gradually lowered and increased temperatures with the following results: of seven fish, one died at 17 °C and none survived at 15 °C more than a few hours; of three fish, two died at 33 °C and one at 34 °C (Dizon *et al.*, 1977; Barkley, Neill & Gooding, 1978). These results on skipjack temperature tolerance support the field observations from the eastern Pacific, but not those from Australia.

Thermal inertia in skipjack depends upon weight (see p. 478). Neill *et al.* (1976) estimated possible upper limits of environmental temperature for skipjack as a function of weight at a normal level of activity. For example, 4 kg and 9 kg skipjack can live in water as warm as 26° and 22 °C, respectively, and only fish of less than 1 kg can tolerate temperatures over 30 °C. Using these estimates and those on the lower temperature limit, Barkley *et al.* (1978) prepared sections and maps of the eastern and central Pacific showing areas and layers suggested as suitable habitats for skipjack of different sizes. They took the limiting concentrations of dissolved oxygen into account as discussed later. They concluded that surface tropical (mixed layer) waters are not a good environment for adult skipjack except at small sizes, and that the normal habitat of large skipjack is the upper thermocline, where it is not oxygen-deficient. They emphasized the need for field testing of their hypothesis. According to Sharp (pers. comm.), skipjack of greater than 1 kg are common in 30 °C waters in some areas, *e.g.*, Papua–New Guinea.

The range of temperature at which bigeye occur was given as 11 to 29 °C by Uda (1957) and 13 to 29 °C by Alverson & Peterson (1963). The higher temperatures represent occurrences in the relatively small surface fishing areas, and the lower temperatures refer to the more extensive range in the longline fishery. Hanamoto (1975) recorded bigeye from 12 to 27 °C, principally in and below the thermocline, in the southern region of the eastern tropical Pacific. This distribution in relation to the thermocline had previously been proposed by Suda, Kume & Shiohama (1969). As shown earlier (see p. 451), bigeye tend to occur deeper than other tunas. The deep longline caught 1·79 times as many bigeye as the regular longline, confirming other indications that abundance increases below the regular longline depth. Bigeye were caught down to 380 m near Fiji and catches in general were higher below 300 m than above. It is clear that the bathymetric limit and hence the lower temperature limit are not yet known for bigeye; it is not known if temperature limits their range.

Much field work has been done to identify range-limiting temperatures for albacore in surface fishing areas of the Pacific. The fish occurrences vary geographically in much the same way as areas of water within a certain temperature range. The lower and upper temperatures suitable for any albacore are about 14° and 23 °C, and the corresponding limits for abundant albacore are 15° and 21 °C, in surface waters (Laevastu & Rosa, 1963; Blackburn, 1965; Laurs & Lynn, 1977, and references). In experimental longlining west of Fiji, Saito (1973) found albacore over the whole range of tested depth, 80 to 380 m. They were most abundant between 200 and 260 m, within the thermocline, where temperatures ranged from 17 to 21 °C. The range of temperature at all depths of capture was 13·5 to 25·2 °C. Other work p. 451) has shown that the vertical distribution of albacore is in general like that of yellowfin, whereas bigeye extend deeper. The deep longline to regular longline catch ratio in albacore is 0·82. It seems, therefore, probable that albacore, like yellowfin, do not occur much deeper than they have already been found. Then the lowest temperature for subsurface albacore may be taken, from Saito's observations, as 13 °C; because this is almost the same as the limiting lower temperature for surface fish it may also be limiting in the horizontal plane. The upper limiting temperature seems to be 25 °C from Saito's data, not 23 °C as found in the temperate-water surface fisheries. Ranges of temperature for the smaller surface albacore and the larger deeper ones appear to be very similar.

The relatively low abundance of albacore along the Equator can be explained, largely, from the range of temperatures in which albacore are abundant. All surface equatorial waters are warmer than 21 °C, except in some areas east of 110° W for a few months of the year. All equatorial waters close to the mean hook depth are either above 21 °C or no higher than 15 °C, except during part of the year between 115° and 140° W (Wyrtki, 1964; Robinson, 1976). Thus the equatorial area is unsuitable or marginally suitable for albacore throughout the year as far as temperature is concerned. Low abundance or absence of albacore in many areas of the eastern tropical Pacific can be explained similarly.

Bluefin in the Pacific have been recorded between 12 and 21 °C, most abundantly between 14 and 19 °C (Uda, 1957; Bell, 1963; see also p. 474). Most of these data are from surface fisheries. We know of no observations on depths or temperatures at which bluefin occur in the longline fishery. Probably the poleward edge of the range of abundant bluefin is temperature-limited, because the species was plentiful farther north than usual along the North American coast during the warm years 1957 to 1959 (Radovich, 1961).

Southern bluefin occur between 10·5 and 21 °C (Robins, 1963), although catches have been made in the northern parts of the West Wind Drift where surface water temperatures reach as low as 8 °C. In the Australian surface fishery almost all the catch is made between 17 and 20 °C, although warmer and cooler waters occur within range of the fishermen (Hynd & Robins, 1967; Williams, 1977).

The foregoing information shows that certain temperatures coincide with and probably determine the limits of the geographical range of certain tunas, including at least yellowfin, skipjack, and albacore. Temperature possibly influences the bathymetric limits in the same species. It is possible, however, that some fish move beyond these limits for short periods. The evidence of limitation by temperature is particularly strong in the case of skipjack, where experimental data confirm the local field observations. These direct effects of temperature upon tuna distribution are confined to determination of range, however, as several authors (*e.g.*, Nakamura, 1951, 1969; Blackburn, 1965, 1969b) have pointed out. Within the range limits of a species, its distribution varies from zero to high abundance in ways that are not related to contemporaneous distributions of temperature as a variable (*e.g.*, Broadhead & Barrett, 1964). As shown later there can be associations between tuna and features of thermal structure such as fronts, but the attractive property of the front is probably biological. Possible causes of patchy tuna distributions in waters of suitable temperature are discussed later (see pp. 490–500).

OXYGEN

Barrett & Connor (1962) suggested that dissolved oxygen concentrations might not greatly exceed the requirements of tunas in warm waters, even at the surface. Blackburn (1965) remarked that dissolved oxygen might limit bathymetric ranges of tunas in some areas where concentrations are very low in the upper 150 m, such as in the eastern tropical Pacific. Experimental data are now available to confirm these ideas for skipjack, which are stressed at concentrations below 2·8 ml/l. Yellowfin, however, are not stressed at 1·4 ml/l (see p. 478). Hanamoto (1975) compared bigeye catches in areas of differing oxycline depth in the eastern Pacific, and concluded that bigeye can tolerate concentrations down to 1·0 ml/l.

Sharp & Francis (1976) presented an equation to estimate the rate of oxygen consumption due to swimming. The swimming rate used in the equation was the minimum required to maintain hydrostatic equilibrium, which was assumed to be the least demanding rate energetically. It varies by species and fish size, and can be estimated for different tunas from data given by Magnuson & Weiniger (1978). Thus, Sharp (1978) could estimate relative rates of oxygen consumption for different species and sizes of tuna and, from the experimental data on lowest tolerable oxygen concentration for skipjack, could estimate such concentrations for other species. The estimated lowest concentrations, varying with fish size, are listed in Table II. These figures for yellowfin and bigeye are, respectively, higher and lower than those obtained from sources mentioned earlier, *i.e.* 1·4 and 1·0 ml/l. The differences are, however, not large and appear quite reasonable in view of the various methods employed.

TABLE II

Estimated oxygen tolerances for tunas of different sizes (after Sharp, 1978, Table V)

Species	Fork length (cm)	Estimated lower oxygen tolerance, 10 min levels (ml O_2/l H_2O)
Katsuwonus pelamis	50	2·45
(skipjack)	75	2·89
Thunnus albacares	50	1·49
(yellowfin)	75	2·32
T. obesus	50	0·52
(bigeye)	75	0·65
T. alalunga	50	1·67
(albacore)	75	1·39

The specified limiting concentration for skipjack would confine the fish to fairly shallow layers in some tropical areas, but temperatures in some of those layers might be unsuitably high for the larger fish. Barkley *et al.* (1978) specified areas and layers that would constitute suitable habitats for skipjack of various sizes in the eastern and central Pacific, assuming a limit of 3·5 ml/l of oxygen and the size-dependent temperature limits mentioned earlier. An example of their findings is reproduced in Figure 16, which represents a meridional section along 119° W in August. Almost all waters above 22 °C have enough oxygen, and are cool enough for skipjack weighing less than 9 kg. Those above 26 °C would be suitable only for skipjack of under 4 kg. The layer between 22 and 18 °C would be suitable for skipjack of all sizes with regard to temperature, but deficient in oxygen at most latitudes. The layer below 18 °C is too cold for skipjack and is also mostly oxygen-deficient. Thus skipjack over 9 kg would find suitable habitat only in the cross-hatched parts of the section (Fig. 16), most of which are subsurface. On the other hand, fish under 4 kg have a much larger habitat available, both in area and depth.

Subject to fuller validation, this hypothesis is useful in explaining and predicting certain features of skipjack distribution. For instance Barkley *et al.* drew attention to large areas west of Mexico and Peru where no suitable habitat for large skipjack could exist. The movement of such fish from coastal waters to the spawning region would then be confined to pathways

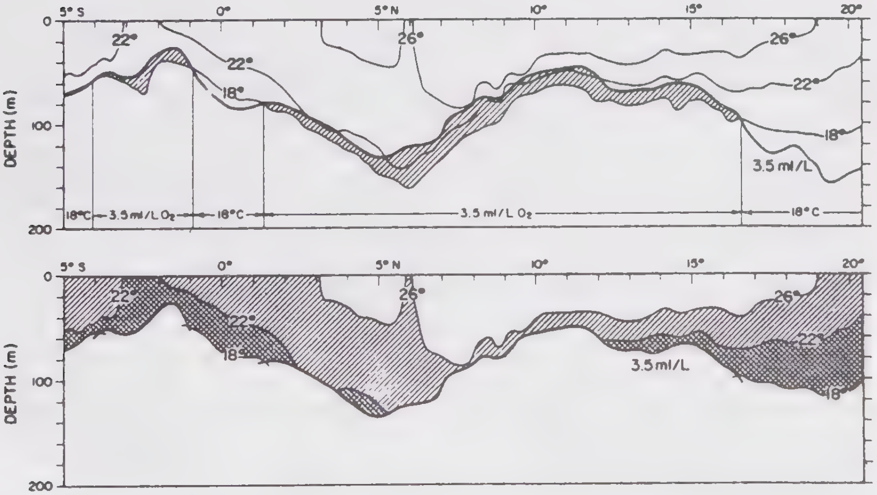

Fig. 16.—Upper panel: temperature and dissolved oxygen (selected isopleths only) along 119° W, eastern Pacific Ocean, August 1967. Lower limits of the skipjack tuna habitat are assumed to be either 18 °C or 3·5 ml/l dissolved oxygen, as indicated; the hatched layer should be warm enough for these fish, but oxygen deficient. Lower panel: hypothesized habitat layers for skipjack tuna of two sizes, 4 kg (entire hatched area) and 9 kg (cross hatched area only) in the same section; fish <4 kg could presumably live anywhere between the sea surface and the lower limits, 18 °C or 3·5 ml/l of dissolved oxygen; from Barkley *et al.*, 1978.

between those areas. Any search for the migrating skipjack should be concentrated in those pathways. The restriction of habitat suitable for large skipjack in the eastern Pacific may explain why the fish caught in the surface fishery near the Americas are generally small, although quite numerous, and why the principal spawning areas are in the central and western Pacific. The depth of the limiting property measurement (temperature or oxygen concentration) is within 50 m of the surface in many parts of the eastern tropical Pacific. Observations by Ingham, Cook & Hausknecht (1977) in the southeastern tropical Atlantic Ocean indicate that oxygen limits the bathymetric distribution of skipjack in other areas besides the Pacific. They found that surface schools of skipjack occurred where the 3·5 ml/l oxygen level was less than 50 m below the surface, with most schools occurring where it was less than 30 m below the surface. This was interpreted as a crowding of fish upwards by the oxygen-poor layer.

Sharp (1978) discussed the question of suitable habitat for both skipjack and yellowfin. For skipjack he recognized the limiting rôles of both temperature and oxygen, in much the same way as Barkley *et al.* (1978). On the other hand, Sharp considered yellowfin habitat to be determined by temperature, since that species can tolerate lower oxygen concentrations (2 ml/l or less) than skipjack. This seems probable to us from the following observations. Mean hook depth in the longline fishery is about 100 m. Yellowfin should become scarce in that fishery where (a) mean temperature at 100 m is below 20 °C or (b) mean oxygen concentration at 100 m is below 2 ml/l. The yellowfin catch per unit fishing effort in the longline fishery is, in general, highest in equatorial waters, but declines in those waters from west to east, starting at about 150° or 140° W (Suzuki *et al.*, 1978). Temperatures and oxygen concentrations at 100 m fall close to the values in (a) and (b) at about those longitudes, and then further decline towards the east as the thermocline and oxycline ascend in the water column. Condition (a) is generally encountered west of (b) at a given latitude, however, because the 2 ml/l level is deeper than the 20 °C isotherm (Muromtsev, 1958; Wyrtki, 1964; Barkley, 1968; Robinson, 1976; Reid *et al.*, 1978). Thus, temperature appears to exclude yellowfin in some situations where oxygen concentration would be suitable. In other situations in the far eastern tropical Pacific, temperature and oxygen are both unsuitable at mean longlining depths.

Bigeye can tolerate 1 ml/l of dissolved oxygen. Concentrations less than that occur at 100 m in several parts of the eastern tropical Pacific where bigeye are hardly ever caught, especially west of southern Mexico and Peru (Wyrtki, 1967; Barkley, 1968; Shingu, Tomlinson & Peterson, 1974; Reid *et al.*, 1978). Oxygen may limit the occurrence of bigeye in those areas, as Hanamoto (1975) suggested. Temperatures at 100 m in the same areas are above 11 °C, which bigeye can tolerate. Some higher temperature may be limiting for bigeye in abundance, but that value is not known. Curiously, yellowfin are taken by longlining in greater quantities than bigeye in some of the areas mentioned, although yellowfin is less tolerant of low temperature and oxygen. The explanation may be that yellowfin are more available than bigeye at hooking depths less than 100 m, as was indicated in the study of bathymetric distribution.

The minimum oxygen concentration for albacore is probably like that for yellowfin, about 2 ml/l, according to the values in Table II. Going from west to east along the Equator, where albacore are scarce, lower oxygen concentrations are encountered at 100 m in some areas east of 130° W (Reid *et al.*, 1978), but at 100 m temperatures are unsuitable for albacore almost everywhere in equatorial waters, as shown earlier. An example of an area with no albacore catch is 10° N: 95° W (Fig. 4). The presumed oxygen limit and the temperature limit for any albacore (13 to 14 °C) are both at about 100 m (Wyrtki, 1964, 1967; Barkley, 1968; Robinson, 1976). There is a layer about 30 m thick within the thermocline where temperature and oxygen both would be suitable, but this habitat may be too restricted for the species to occur abundantly. If it were to occur, it would not often be taken on the longline because few hooks would hang in such a shallow layer. We wish to emphasize a point made elsewhere: that because oxygen and temperature values are suitable does not mean that tunas will be present. Absence of favourable water properties does mean exclusion of the fish, but presence of favourable waters does not mean presence of fish.

No information on oxygen requirements of bluefin or southern bluefin is available. We conclude that the known bathymetric ranges of the other four species, and thus some features of their geographic ranges in the subsurface fishery, can be explained from vertical distributions of temperature or dissolved oxygen or both. The clearest cases are for skipjack, where both properties set the range limits, and yellowfin, where temperature alone does so.

SALINITY

Atlantic bluefin tuna (*Thunnus thynnus thynnus*) occur in waters with salinity ranging from 18 to 38‰ in the Mediterranean and Black Seas (Tiews, 1963). This is almost the entire range of salinity in the world oceans. Except for the report of Laurs, Yuen & Johnson (1977) on ultrasonic tracking experiments with albacore noting that a change in the orientation of albacore was observed at a weak salinity front, other comparisons of salinity and tuna distributions suggest a lack of relation. Scarcity of tuna near river mouths might be explained by turbidity. Blackburn (1965) considered that salinity by itself has no direct effect upon tuna distributions at or within the range limits, and that statement has not been challenged. Salinity also seems not to determine distributions of other pelagic oceanic animals (Kinne, 1971; Holliday, 1971). Barkley (1969) noted that adult skipjack occur in areas of the Pacific where there is a shallow salinity maximum permanently or seasonally, or where the salinity maximum is at the sea surface. The two kinds of areas together cover the entire tropical and subtropical Pacific. It was not claimed that the actual salinities or the maximum were directly related to the skipjack distribution. Donguy, Bour, Galenon & Gueredrat (1978) and Bour & Galenon (1979) noted a strong correlation between the catch of surface tunas and salinity in the western Pacific. Dizon (1977) observed no changes in swimming speed or in any other behaviour of captive young skipjack and yellowfin as salinities were reduced from 34 to 29‰.

Seckel (1963, 1972) found an association between salinity and skipjack at Hawaii, the fish being most abundant when salinity is below 34·8‰. These lower salinities are an indicator of water of the California Current Extension, which is a tributary of the North Equatorial Current. Migrating skipjack from the east approach Hawaii in the North Equatorial Current, as mentioned elsewhere. In winter, and in summer of some years, this low-salinity water does not reach Hawaii and skipjack are scarce there. The salinity does not determine the distribution of skipjack at Hawaii but it is a useful indicator of the current, which does.

TRANSPARENCY

Tunas locate food objects principally by vision, and perhaps also by olfaction (Magnuson, 1963, and references; Nakamura, 1962). Turbid waters should, therefore, be rather unsuitable for them, although extremely clear waters would contain little food. Reid *et al.*, (1978) gave a map of Secchi disc depths in the equatorial and North Pacific, based on data from Frederick (1970) and other authors. It shows that Secchi depths in the geographic range of tunas (*i.e.*, to 40° N) are generally between 15 and 50 m, with the highest readings in the anticyclonic gyre of the central North Pacific. North of 40° N the waters are less clear with Secchi depths generally below 15 m. Secchi depths under 15 m indicate high concentrations of terrigenous or phytoplanktonic particles near the sea surface. Where these particles are phytoplanktonic, the chlorophyll concentrations are over 0·8 mg/m^3 (Forsbergh, 1969). Such chlorophyll concentrations in tropical and subtropical waters are virtually confined to coastal upwelling areas, which are frequently too cold for tunas as shown later in this section. If low transparency of water directly restricts the habitat of tunas, it is probably in coastal areas that are kept turbid with particles washed or blown from the land, and such processes as waves and tides which stir up shallow water. There are such areas where tunas are absent or rare, although other conditions such as temperature and food appear satisfactory for them. Bass Strait, between the Australian mainland and Tasmania, is an example (Blackburn & Serventy, in press).

CURRENTS

It was suggested by Nakamura (1954) that different tuna species have their centres of distribution or characteristic habitats in different currents. The idea arose from earlier studies of variations in apparent abundance of species in the Japanese longline fishery, especially in the western Pacific where that fishery originated. The examples most commonly mentioned were yellowfin and bigeye, considered to be most abundant in the South Equatorial Current and North Equatorial Countercurrent, respectively. The idea appeared less satisfactory as the fishery spread across the Pacific and into other oceans; the known ranges of the species were extended considerably northwards and southwards, and overlapping was seen between areas of maximum abundance for different species. In addition, it was not clear why the postulated relations with the currents should be expected. Doubts about the suggestion were expressed by Blackburn (1965). Nakamura (1969) replied to the objections, and appeared to concede that the species were indeed distributed more broadly and in a less segregated way than he had originally suggested. He described more instances of tuna migrations between currents than within them.

Blackburn (1965) also noted that several other authors had written rather casually about relations between tunas and currents, without specifying what the relations were. He thought some of the tuna distributions in the Kuroshio Current and Gulf Stream might be determined by temperature instead of by the current. He also pointed out that tunas exhibit swimming speeds in the range of 15 to 50 km/day (Clemens, 1961; Anonymous, 1977; Laurs *et al.*, 1977; see also Dizon, Brill & Yuen, 1978), which would enable them to move independently of currents or with them (Sharp & Vlymen, 1978).

Seckel (1972) took a mechanistic approach when discussing the relationship between migration and currents in that the term migration means simply that a fish is in one location at one time and in another location at another time. He expressed this relationship as follows. The distance covered by the fish or schools, S, during a time interval Δt is $\Delta S = V\Delta t$, where V is the velocity of the fish. The velocity of the fish is the velocity of the water (W) carrying the fish (current) plus the velocity of the fish (F) swimming relative to the water, that is

$$V = (V_W + V_F).$$

Thus, the distance covered becomes

$$\Delta S = (V_W + V_F)\Delta t.$$

Over a period of time, the migration distance is the sum of these elements

$$S = \sum_{i=1}^{n} [(V_W + V_F)\Delta t]_i.$$

In short, all fish migrations contain these elements and, therefore, currents are a part of all migrations except when $V_W = 0$, a rare occurrence.

When V_W is much less than V_F, V_W may possibly be ignored. When the migration time is long, however, even if V_W is much less than V_F, $V_W\Delta t$, the distance the fish is carried by the water, may not be negligible. Therefore, it is not unreasonable to have a first impression such as that of Nakamura. Subsequent spread of the fishery illustrates that the additional component V_F is also present. One also might consider the fact that current speeds and direction at the ocean surface are not necessarily the same as at depth, particularly at the depths occupied by deep swimming bigeye.

As mentioned on p. 455, Seckel (1972) and Williams (1972) invoked currents to account for movements of skipjack between the eastern and central Pacific. Seckel concluded that the movement of adults from the eastern Pacific to Hawaii could be explained by random swimming and drifting in the North Equatorial Current. He said, "An attractive aspect of the drift hypothesis is its simplicity. Skipjack while in the North Equatorial Current need not do, know, or remember anything other than to search for food." These westward-moving fish do not, as far as is known, return later to the eastern Pacific. Movement from the central to the eastern Pacific is thought to occur only when skipjack are very young, and Williams (1972) has considered ways in which it could take place. His three models assume either a passive drift with currents or an active movement against them.

In addition to the direct effects of currents on the distribution of tunas, currents affect the distribution of prey and the distribution of temperature and thermocline topography and, therefore, indirectly affect the distribution of tunas. Hanamoto (1974) considered that the Equatorial Undercurrent affects the apparent abundance of bigeye in the far eastern Pacific by preventing longline hooks from sinking to normal depths.

WATER MASSES

A few authors have attempted to explain geographical distribution of tunas from distributions of water masses (bodies of water characterized by specific temperature-salinity relations), but none have been very successful. Yamanaka, Morita & Anraku (1969) considered that Pacific bluefin and albacore were distributed according to water masses at particular stages of their life history, but not in the same way at all stages. At times when tunas do appear to show close association with water masses, it is quite likely that some other property or feature of the water actually determines the tuna's occurrence. For instance, Laurs & Lynn (1977) considered that temperature and food conditions in the Transition Zone actually determine the uneven occurrence of the albacore.

FOOD AND FOOD CHAINS

Thus far, we have identified properties that limit the total range of tunas, by area (temperature and possibly transparency) and depth (temperature and oxygen). These properties do not account for differences in abundance of adults within the ranges. It seems likely that some major differences of that kind are due to tuna travelling in particular current systems, but even those systems are very large and tuna do not occur uniformly within them. It has often been suggested that tuna tend to be most abundant where their food is concentrated, within areas of suitable temperature. Blackburn (1965, 1969b) strongly supported this view.

The food of tunas in nature has been much studied from stomach contents, with very consistent results. It consists in general of active pelagic animals measuring from about 1 to 10 cm: fishes, molluscs, and crustaceans. Micronekton is a convenient term for this group, although some of the organisms, such as euphausiids, are generally considered as plankton. Much of the literature on tuna food up to 1963 was cited by Blackburn (1965). Important later papers include Williams (1966), Dragovich (1969), Dragovich and Potthoff (1972), and Legand *et al*. (1972). The first of these deals with Indian Ocean yellowfin and the next two deal with Atlantic tunas.

The tunas do not, however, eat all kinds of micronekton that are within their ranges. Two major groups by biomass that are little consumed are the mesopelagic fishes which migrate from deeper waters towards the surface at night, especially Myctophidae and Gonostomatidae, and euphausiids. An exception to the first is the gonostomatid genus *Vinciguerria*, which is eaten significantly (Alverson, 1963; Legand *et al*., 1972). Probably the tunas cannot see prey well at night. *Vinciguerria* moves upwards at night, but lives within the vertical range of tunas in the daytime (Legand *et al*.). Another exception is the significant eating of certain euphausiids by skipjack in some areas, such as off Ecuador (Alverson, 1963) and Tasmania (Blackburn & Serventy, in press). Skipjack may be better than other tunas at sensing, catching, and retaining euphausiids. The mean gillraker gap is smaller in skipjack than in several other species (Magnuson & Heitz, 1971). Cushing (1976) cited myctophids → tuna and euphausiids → tuna as steps in food chains in the tropical and subtropical ocean, and gave no other examples at those trophic levels. These statements describe exceptional rather than typical cases and, therefore, are misleading.

In general, then, tunas eat epipelagic fishes, molluscs, and crustaceans, including the larvae of those groups. They are opportunistic feeders, swallowing whatever moving small objects they can see (Blackburn, 1968). It is not clear how they sense and take dead bait in longlining operations at depths greater than 300 m, where very little light is available. Olfaction is possibly involved in that case.

The distribution of micronekton has been little studied quantitatively in the ocean. Estimates of standing stock can be obtained, with difficulty, from catches made in various large nets in a few parts of the Pacific (King & Iversen, 1962; Vinogradov, 1968; Blackburn, Laurs, Owen & Zeitzschel, 1970; Legand *et al.*, 1972). With euphausiids included, values in the 0–200 m layer are approximately 0·6–1·0, 0·3, and 0·6 g/m^2 in tropical, subtropical, and subarctic waters, respectively (Blackburn, 1977). These estimates must be too low, because it has been found repeatedly that nets do not capture most epipelagic fishes and molluscs efficiently, except as larvae. King & Iversen (1962), Blackburn (1968), and Legand *et al.* (1972) all noted that those groups were much better represented in tuna stomachs than in net catches—presumably because they can avoid nets. The nets appeared good only for catching mesopelagic fishes, crustaceans, and larvae. We have no reliable biomass estimates of the part of the micronekton not taken by the nets. Thus the concentrations estimated from the nets include much that tuna do not eat and omit much that they do eat. Laurs & Nishimoto (in prep.) found a direct relationship between the displacement volume of food in the stomachs of albacore and the biomass of micronektonic animals taken with the Isaacs–Kidd Midwater Trawl in the same area, although the species composition in the stomachs and net hauls were different.

It seems certain, however, that the general ocean-wide distribution of micronekton is broadly similar to that of nutrients (Reid, 1962), phytoplankton (Koblentz-Mishke, Volkovinsky & Kabanova, 1970), and zooplankton (Bogorov *et al.*, 1968); that is, high in subpolar and upwelling regions, moderate in other coastal and equatorial regions, and low in the anticyclonic gyres. The agreement between these steps in the food chain probably holds within these parts of the ocean as well as between them. In the eastern tropical Pacific, standing stocks of net-caught micronekton and zooplankton are positively correlated (in logarithms and with the micronekton measured four months later; Blackburn, 1973). In the waters where most tunas live, biological productivity ranges from moderate to low. Regions of high productivity tend to be too cold for them, except in equatorial and other tropical upwellings.

On the other hand, tunas are fairly heavy feeders. Captive skipjack fed to satiation ate 15% of their body weight per 12 h day (Magnuson, 1969). Feeding experiments with other fish species, mostly fed to excess, indicated daily rations generally less than 10% of body weight, although up to 24% was noted in the scombroid *Pneumatophorus japonicus* (Conover, 1978). A similar tendency is evident from published estimates of rations, based on bioenergetic demand. Sharp & Francis (1976) estimated the required daily ration as 10% of body weight for yellowfin 45 cm long, declining gradually to 3% for the same species at 140 cm. Other tunas under 40 cm can eat more than 30% of body weight per day (Sharp, pers. comm.). By contrast, the estimated daily rations for the pelagic fish community of a coastal upwelling area, predominantly planktivorous carangids and clupeoids, ranged from 4–8% of the body weight (Mathisen, Thorne, Trumble & Blackburn, 1978).

Despite the high daily food requirements of tunas, the migratory life style of these fishes is obviously very successful even in the open ocean where there is a highly patchy distribution of forage at all trophic levels (Magnuson & Heitz, 1971; Kitchell *et al*., 1978). Magnuson & Heitz (1971) also commented on the occurrence in a given habitat of a resident population(s) present throughout the year, and a seasonal influx of other individuals and species. The resident population is supported by the lowest expected level of productivity, whereas the seasonal influx is synchronous with seasonal productivity resulting from variable oceanographic phenomena such as upwelling. Sharp & Francis (1976) and Kitchell *et al*. (1978) have emphasized this 'bottleneck' of lowest expected productivity and how it may affect, in particular, the early stages of tunas. The pre-spawners of many tunas are highly migratory and hence oceanographic events can have major effects on stocks, such as growth rates. Dotson (1978), in his work on north Pacific albacore, has shown the fluctuations of fat content in tunas and how they are associated with different behavioural patterns or stages in the life history. Kitchell *et al*. (1978) were unsure that the attainment of the "maximum daily ration" in tunas is quite so spectacular as implied by their habitation of one of the most unproductive environments—the epipelagic zone of the tropical seas, given the broad feeding habits of tunas, the amount of food which they can take in a given period, and the inaccuracy of estimates of potential forage based on trophic relationships.

It seems likely, therefore, that movements into relatively productive areas may have survival value for tunas, and that they probably aggregate at any rich patches of food that they find in waters of suitable temperature. The next two sections of our review give some support for these ideas, based upon observations in the field. To make a more definite statement about tunas' food requirements in relation to the food available in a given area, the following kinds of information would be needed: (i) biomass of tunas; (ii) biomass of all other animals, such as certain billfishes and porpoises, that eat the same kinds of food as tunas; (iii) amount of food required per day by all those animals; and (iv) daily production of the food organisms. None of this information exists at present. Sharp & Francis (1976) attempted to solve the problem in the eastern tropical Pacific. They estimated (i) and thence (iii) for yellowfin only, ignoring all other tunas, billfishes, *etc*. Item (iv) was not specifically estimated, but the authors considered it was higher than their (iii). It is not quite clear how they reached that conclusion, but it was apparently based upon the biomass of net-caught micronekton and some unspecified estimate of its turnover rate. Such biomass measurements are unreliable as measures of tuna forage, for reasons already stated. This work is, therefore, unconvincing. By contrast, in the above-mentioned study of a fish community made by Mathisen *et al.* (1978), it was found possible to measure the total fish biomass (equivalent to (i) plus (ii)) acoustically, thence estimate (iii), and to estimate (iv) from the measured biomass of zooplankton together with production/biomass ratios taken from literature. In that case (iv) exceeded (iii), as might be expected in a coastal upwelling area, but one could not assume that result for tuna habitats in general. Similar studies on tunas should be continued as adequate measurements or estimates become available for the biomass of the tunas, their competitors, and their prey.

UPWELLING AND VERTICAL MIXING

Physical processes that may enrich near-surface waters with nutrients are considered here. They include wind-induced upwelling (coastal and equatorial), geostrophic upwelling, and vertical mixing by wind. The enrichments will lead to the appearance of higher than average standing stocks of micronekton, either at or downstream from the upwelling or mixing site. Tuna are expected to be plentiful in those areas because of the micronekton, unless the waters are too cold or turbid.

In a non-tropical upwelling situation the rich forage (food supply) should

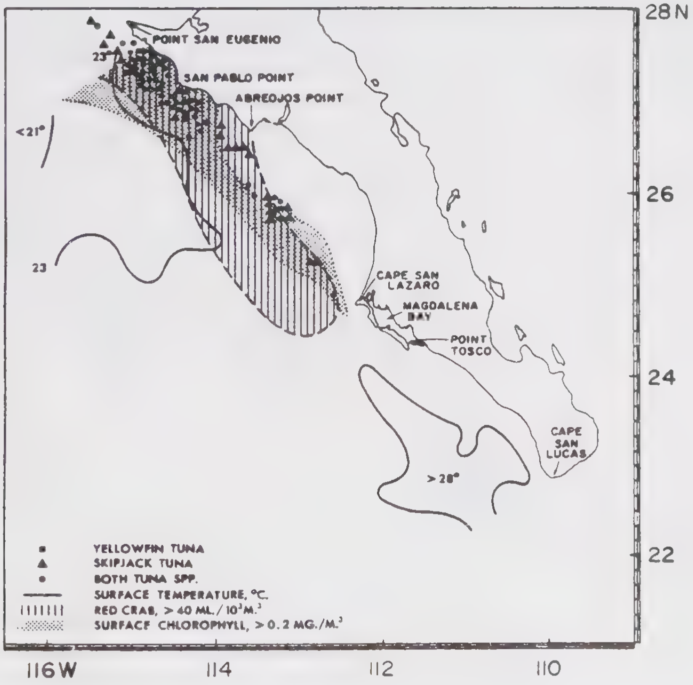

Fig. 17.—Distributions of surface temperature, surface chlorophyll *a*, and red crabs in September, 1965 and locations of contemporaneous tuna catches; from Blackburn, 1969.

attract tunas, but the low temperatures may exclude them from it. This was shown well in studies made at different stages of the coastal upwelling off western Baja California (Blackburn, 1969a). Advantage was taken of the fact that yellowfin and skipjack in that area eat predominantly one species, the red crab, *Pleuroncodes planipes*, which can be sampled quantitatively with micronekton nets. The crab, a herbivore, is most abundant in the upwelling areas where the highest phytoplankton stocks occur. When the upwelling is strong, surface temperatures in those areas are below 20 °C and the tunas can, at best, reach only the fringes of the high crab concentrations. The fish aggregate at these fringes, obtaining some food at temperatures they can tolerate. As the upwelling regime decays, the food-rich areas become warm enough for the tunas to penetrate them. The distributions of tuna, crab, and phytoplankton then tend to become congruent in the former upwelling areas (Fig. 17, from Blackburn, 1969a). Finally, the same three distributions become uniform over most of the area west of southern Baja California, until the normal seasonal cooling drives the tunas southwards.

Similarly, albacore in the northeast Pacific approach the edges of coastal upwelling areas, presumably to feed, but they avoid the upwelled water where it is colder than 15 °C (Laurs *et al.*, 1977). Farther offshore, they are confronted with the same problem of forage-rich waters tending to be too cold. They apparently avoid Subarctic water, where food is plentiful (from vertical mixing) but temperature is too low, and also Central water, where food is scarce and temperature varies from too high to suitable. The Transition Zone between the two types of water contains food at an intermediate level of abundance, and has suitable temperatures in the albacore season, and it is there that most albacore are found (Laurs & Lynn, 1977; Fig. 18).

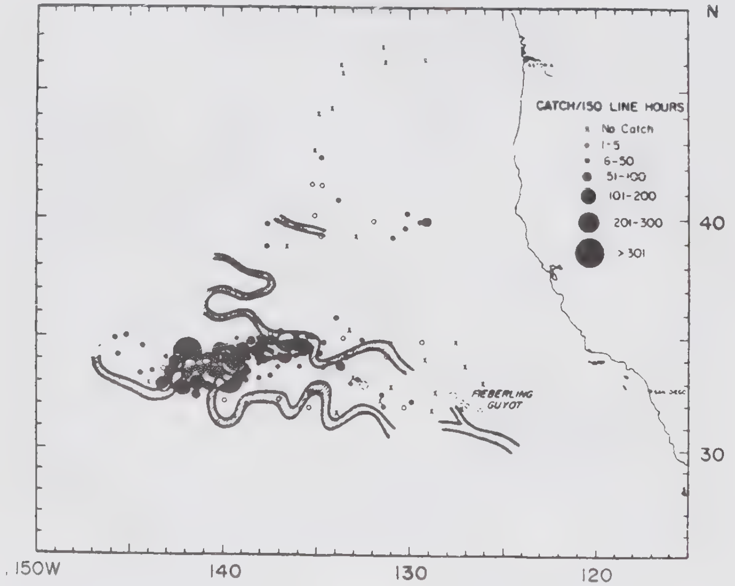

Fig. 18.—Albacore catch per 150 line-hours by charter fishing vessels and locations of fronts delineating the Transition Zone waters during June, 1973; from Laurs & Lynn, 1977.

In tropical upwellings, temperatures at the surface are usually suitable for tunas. Blackburn (1962, 1963) described the upwelling situation (although he did not call it that) in the Gulf of Tehuantepec. Yellowfin abundance increased three months after the upwelling, the lag being attributed to the production of an increased biomass of micronekton. Forsbergh (1969) investigated the upwelling in the Gulf of Panama and the apparent relation of yellowfin and skipjack to it. He considered the conditions to be practically the same as in the Gulf of Tehuantepec.

The distribution of subsurface yellowfin in relation to the equatorial upwelling in the Pacific has been discussed by several authors including Sette (1955), and reviewed again by Murphy & Shomura (1972). The fish are more abundant between 1° and 6° N than at the Equator where the upwelling is centred. The explanation given is that the major drift of newly upwelled water is towards the northwest. Organisms develop in this water, those at successively higher trophic levels reaching their biomass maxima at successively longer intervals of time. The biomass maximum of the micronekton tuna should be, therefore, a few degrees north of the Equator, with tuna aggregated on the forage. This expected forage maximum was found (King, 1958; King & Iversen, 1962).

Blackburn & Laurs (1972) suggested that skipjack might also be related to the equatorial upwelling through their food. These authors charted the distribution of total biomass of all skipjack prey organisms, which were sorted from micronekton net catches made on several cruises in the offshore waters of the eastern tropical Pacific. Three zonal maxima were noted, the one just north of the Equator already mentioned, another just south of the Equator, and a third in the latitudes of the North Equatorial Countercurrent. The first maximum was much better defined than the others. The second was assumed to be formed in the same way as the first but under conditions of southwesterly drift. The third was thought to result from vertical mixing over a ridge in the thermocline along the north edge of the Countercurrent. Two cruises were made to test the hypothesis that skipjack would be most abundant in those areas (Blackburn & Williams, 1975). On the cruise both skipjack and its forage were most abundant just north of the Equator and no other zonal maximum of either was seen. On the other cruise skipjack were more abundant north of the Countercurrent than near the Equator, but the forage distribution was the reverse.

FRONTS

Fronts are boundaries between waters of different densities, recognizable by strong gradients of temperature and/or salinity. Fronts at the sea surface may also at times be recognized by differences in colour or turbulence between the waters and by lines of flotsam. They have important effects on tuna distribution. A knowledge of fronts is valuable to fishermen in the surface tuna fisheries, probably more so than any other kind of oceanographic information except surface temperature. Some fronts, really frontal systems, are a few hundred kilometres wide. Examples are the Transition Zone in the northeast Pacific, previously discussed in relation to albacore, and the corresponding zone between the Kuroshio and Oyashio Currents in the northwest Pacific, which is also an important area for tunas (Uda & Ishino, 1958).

Other fronts vary in width from a few tens of kilometres to tens of metres. The smaller they are, the less permanent and more variable in position they tend to be.

When a temperature front contains the isotherm that limits a tuna's range, the front constitutes a simple barrier. This occurs at times in the Cape San Lucas front off Baja California (Blackburn, 1969a) and in 'upwelling fronts' along the offshore boundary of coastal upwelled water (Laurs *et al.*, 1977). On the other hand, it is common to find tuna aggregated at a front, under conditions in which the range of temperatures in the general area is suitable (*e.g.*, Williams, 1977). The question in that case is, what causes the tuna to be abundant at the front? Investigators believe food is responsible, being more abundant at the front than elsewhere. Dufour & Stretta (1973) pointed out that this could occur in three ways: mechanical accumulation of plankton because of convergence at the front, higher biological production because of divergence near the front, and higher production because of the mixing of waters with complementary characteristics.

Few attempts have been made to demonstrate the expected high abundance of tuna prey in fronts. The best instances known to us concern the Cape San Lucas front in the eastern Pacific (Griffiths, 1965; Blackburn, 1969a) and the Cape Lopez front in the eastern Atlantic (Dufour & Stretta, 1973). Each front is on the order of tens of kilometres wide. Chlorophyll *a*, zooplankton, and micronekton (taken in nets) were sampled during synoptic crossings of each front: on the warm side, on the cool side and in the middle. At the Cape San Lucas front chlorophyll and some kinds of zooplankton were most abundant as biomass in the middle of the front. Micronekton biomass was highest on the warm side, except at a part of the front where the cool side was upwelled and had the most micronekton. Yellowfin tuna, when present near the front at the times of these observations, were on the warm side; temperatures in the front and on the cool side were too low for them. At the Cape Lopez front, chlorophyll showed a gradual decline across the front region from the cool to the warm side. Zooplankton (by numbers, mostly copepods) were most abundant in the middle. Micronekton were most abundant by numbers in the middle, but by biomass they were slightly more abundant on the cool side than in the middle. Yellowfin and skipjack were most abundant in the front, although temperatures on both sides of it were also suitable.

The above-mentioned differences in chlorophyll, zooplankton, and micronekton across each front were not large, seldom more than half or double, and could therefore be questioned. More observations are desirable. It appears significant to us that zooplankton, the animals most likely to be mechanically accumulated, were most abundant in the middle of each front. Micronekton, being stronger swimmers, are less likely to be concentrated in the same way. They could be attracted to the front by the zooplankton, but perhaps not all of them at the same time. It must also be remembered that micronekton nets are poor samplers of tuna forage. The data available do not show beyond doubt that tuna forage is more abundant in fronts than in adjacent waters, although Dufour & Stretta's (1973) observations give indications that it is.

Laurs *et al.* (1977) described movements of three albacore which were tagged and tracked with ultrasonic equipment. It appeared that the fish remained close to 'upwelling fronts' when they existed, but moved away from the area where the front was located when upwelling ceased and the front was no longer apparent at the surface. The fish avoided temperatures of less than 15 °C. There was an interesting indication that the fish tended to move slowly when crossing fronts. A deliberate response of that kind to the temperature gradient is possible, because tunas can perceive changes as small as 0·1 °C (Steffel, Dizon, Magnuson & Neill, 1976). The response also could have been to food organisms, if any were present.

ISLANDS AND BANKS

Surface-swimming tunas are often more abundant around these features than elsewhere in the same part of the ocean. It has generally been assumed that more food is available on or around the banks and islands, or in associated fronts and eddies. Some attempts have been made to demonstrate such distributions of food, with mixed results. Blackburn (1965) briefly reviewed some of the literature. Although the food hypothesis is reasonable, it may not explain all cases. In the central tropical Pacific the association between tuna and islands is much more obvious for yellowfin than for skipjack (Murphy & Ikehara, 1955; Murphy & Shomura, 1972). The occurrence of skipjack at the Hawaiian Islands can be explained partly by their arrival in a current, as mentioned earlier. Japanese tuna fishermen note that fishing grounds form on the upstream side of banks and sea mounts (I. Yamanaka, pers. comm.). Tuna fishing off Baja California is often particularly successful at banks, but Blackburn (1969a) showed that some of these instances could be explained by food-rich upwelled water (when not too cold) enveloping the banks. It is also possible that islands and banks are attractive to tunas as points of orientation.

PORPOISES

In the offshore waters of the eastern tropical Pacific surface fishery, co-occurrence of porpoise and tuna is considered vital to fishing success. Purse-seine fishermen use the sighting of birds as an indication of the presence of tuna. At times porpoise are also present, and if so they are surrounded and both the porpoise and tunas are captured. The porpoise then are liberated and the tunas brought aboard the boat. There are instances that porpoise are observed without the presence of birds, and they are also checked for the presence of tunas, and the operation is similar if fish are present.

Two species of porpoise, *Stenella attenuata* and *S. longirostris*, are especially important in the tuna fishery. The cause of the tuna–porpoise association and why the association appears to vary in strength between species and years is unknown. Yellowfin and *S. attenuata* eat many of the same kinds of food and may feed together, but the diet and feeding habits of *S. longirostris* are different (Perrin, Warner, Fiscus & Holts, 1973). The area of the porpoise–tuna association in the eastern tropical Pacific is essentially coincident with that of the yellowfin surface fishery. Many of the environmental features that appear important to yellowfin appear similarly important to these porpoise. The habitat of the porpoise extends beyond the area of the surface fishery, but the porpoise–tuna association is primarily in the latter area where environmental features such as temperature and oxygen may result in feeding interactions near the surface between porpoise, yellowfin, and birds (Au, Perryman & Perrin, 1979).

PREDATORS

Apart from man, the only known predators of large adult tunas in nature are billfishes, especially blue marlin (*Makaira mazara*) and black marlin (*M. indica*) (Royce, 1957). Sharks and killer whales (*Orcinus orca*) eat tunas that have been caught or injured in fishing operations. Tuna larvae and juveniles are eaten by billfishes, adult tunas, and probably many other animals. Skipjack larvae and young juveniles are a significant part of the diet of adult skipjack in some regions (E. L. Nakamura, 1965; Kearney, 1978).

ENVIRONMENTAL REQUIREMENTS OF TUNA LARVAE AND JUVENILES

It was shown previously that the patchy distribution of adult tunas within a suitable habitat is probably related very largely to forage, whose distribution can be explained in relation to physical features such as upwellings and fronts. Another possible determinant of adult tuna distribution, during spawning seasons, is the needs of their larvae.

Very little information exists on larval requirements. As mentioned earlier (see pp. 465–472) the spawning areas of most investigated tunas are in near-surface tropical waters, and tuna larvae are most abundant at the high end of the species' temperature ranges. The warm waters appear most suitable for larvae, but must often be relatively poor in food for adults. Adults will not always be found in the most forage-rich areas. They must sometimes leave them in order to reproduce effectively. In the case of southern bluefin, the tropical spawning area is far removed from the high-latitude waters which seem to constitute the principal habitat of the adults.

With skipjack and albacore the areas of highest larval abundance are only in certain areas of the tropical Pacific, for instance, not in the eastern Pacific for skipjack (although temperatures suitable for larvae are available) and not in equatorial waters for albacore. These areas with few or no larvae are physically unsuitable for the parent fish (large adults of skipjack, all adults of albacore) as shown earlier.

No investigator has yet successfully described the vertical distribution of young stages of tunas. These distributions are probably not uniform, and as has recently been learned for coastal pelagic fishes (Lasker, 1978), the survival of larvae and juveniles is largely dependent on their distribution being coincident with that of patches of their food. Seckel (1969) showed the presence of a layer of high oxygen concentrations, which is probably of biological importance, at depths of around 50 to 100 m in the North Pacific. This layer is in the upper thermocline, and is likely to be formed as a consequence of high productivity. High zooplankton and micronekton concentrations would also be expected in nearby layers, but would not be detected by the usual sampling method of obliquely hauled nets. In fact, detection of layers or patches of concentrated plankton has been, and is, a persistent problem in marine biological investigations.

It is a characteristic of tunas of many species that up to 40–70 cm in length they school together in surface waters. At this size range the juveniles attain the morphological and physiological adaptations which result in ecological stratification and the constituent species of the mixed schools rapidly disperse to their respective adult strata. There is little information on the location of juvenile tunas, especially those less than 40 cm. The problems of field sampling to define their distribution become obvious when one considers that a 50 cm specimen of even the slowest swimming tuna must travel the equivalent of 27 km per day for hydrodynamic equilibrium, and a skipjack about 60 km per day. Migratory behaviour of pre-spawners in general, and their occurrence in areas of high productivity and high vulnerability, indicates an ability to sense and perhaps 'climb' environmental gradients (Neill *et al.*, 1976) and food gradients (Williams, 1972). Such behaviour may prove useful in future attempts to define their distributions in more detail than is at present possible.

AGGREGATION OF TUNA AROUND FLOATING OBJECTS

Tuna fishing in the immediate vicinity of anchored or free-floating objects has gone on for many years. Occasionally, large catches have been made in the proximity of floating objects using surface gear. Bamboo rafts are used in Japanese waters, vertical arrays of palm fronds are set out in the Philippines and Indonesia, and cork slabs are used in the Mediterranean Sea. Japanese fishing vessels are at times reported to transport floating materials to the fishing grounds of the western tropical Pacific and to set them adrift there for the purpose of attracting tunas for capture. The new purse-seiners from Japan set their nets around floating logs or other objects whenever such are available in the western Pacific. Experiments were conducted during 1972 and 1974 in Papua–New Guinea waters on the attraction of artificial floating objects to skipjack (Yamanaka, Yukinawa & Morita, 1977). Floating objects encountered by the surface tuna fleet in the eastern Pacific have long been routinely investigated for the presence of fish (Greenblatt, 1979). In the past few years, the National Marine Fisheries Service Honolulu Laboratory has conducted experiments in Hawaiian waters on the attraction of anchored floating 'buoys' to tunas.

Reports have been published on the sequential occurrence of fishes of numerous kinds and their behaviour under floating, drifting rafts and objects (*e.g.*, Kojima, 1956; Hunter & Mitchell, 1967, 1968; Wolf, 1974). Attempts to observe and explain events related to tuna behaviour and to the attractiveness of various floating object configurations have been made and reported on by Gooding & Magnuson (1967), Hunter & Mitchell (1967, 1968), and Inoue, Amano, Iwasaki & Yamauti (1968). Hypotheses advanced to explain the accumulation of fishes around inanimate floating objects include the following: (1) fish seek shelter from predators; (2) larger fish gather to prey upon concentrations of smaller fish; (3) fish feed on algae and decaying material from the 'raft'; (4) fish seek shade under the object; (5) fish use floating objects as a substratum on which to lay their eggs; (6) the shadow of the objects makes zooplankton (forage) more visible to fish; and (7) floating objects are cleaning stations.

Gooding & Magnuson (1967) considered these hypotheses and concluded that no single one could explain the occurrence of fishes around floating objects at sea. They thought that the shelter hypothesis (1) was the best substantiated of those listed. Obviously, some of them cannot pertain to tunas (*e.g.*, 3, 5, and perhaps 7). Wolf (1974) observed that the "attraction of fish appears to be due to random encounter with the drifting object and while chances of such encounters may be slightly increased by an increase in the size of the surrounding fish aggregation, the removal of some fish does not seem to affect the overall attractiveness of the object". Hunter & Mitchell (1967) also remarked on the mechanism of encounter, stating that most naturally occurring objects did have fish around them and were located in areas of current convergence. These two latter observations bring to mind important questions which remain unanswered with respect to tunas and free-floating objects: (1) whether the objects and the tunas move together with the currents and accumulate (passively) in areas such as convergences (Seckel, 1972; Williams, 1972), or (2) whether the tunas seek and encounter the objects and thus accumulate (actively) in their proximity? The latter possibility would apply to anchored objects as well (Klima & Wickham, 1971). Further testing of the hypotheses seems feasible in the near future through application of available technology involving radio and satellite tracking of fish and drifting objects.

RECENT ADVANCES IN PRACTICAL APPLICATION OF TUNA OCEANOGRAPHY TO FISHING AND IN THE USE OF REMOTE SENSING FOR COLLECTION OF THE NEEDED OCEANOGRAPHIC DATA BASE

Scientific and technological observations on the environment and the behaviour of tuna (or other fishes) and hypotheses on their interdependence are of direct value to fishermen, but are rarely available to them. Such information is worked-up by fisheries environmental services into various more suitable formats for transmission to the fishing fleets (and industry generally, *e.g.*, processors) so as to assist in the development and optimal utilization of their resources. The data base for such advisory services is increasingly being supplemented by oceanographic information derived from remote sensing techniques (using aircraft or satellites as observation platforms). To date, most services have exclusively attempted to relate fish distribution and water temperature (Tomczak, 1977); given the importance of water temperature to tunas, it is not surprising that many of the fishery environmental services have been developed for tuna fisheries. The fisheries environmental services usually are of two kinds (Tomczak, 1977): (a) analyses and short-term forcasts for tactical use by fishing fleets, and (b) medium to long-term forecasts for strategic use.

There are at least six fisheries environmental services dedicated (or partly so) to supporting tuna fisheries and most are concerned with short-term tactical forecasts. Two services are operated for the eastern Pacific Ocean by the National Marine Fisheries Service, La Jolla, California. These are as follows.

(1) In the surface purse-seine fishery for yellowfin and skipjack many tactical fishing decisions are made, based in part, on daily charts of weather

and sea state and weekly charts of sea surface temperature and mixed layer depths transmitted by radio facsimile (see Evans, 1977, for details). The information is from analyses based on mixed source data bases, including remote sensing (meteorological satellites), and marine weather and temperature at depth (from expendable bathythermographs) direct from the fishing fleets.

(2) Similarly, in the northeast Pacific albacore fishery, daily and biweekly advisory forecasts are made to the boats with information on fishing activity and location, surface and subsurface temperatures, marine weather, *etc*., which can be used for tactical advantage. In addition, a pre-season forecast is made of the expected geographic distribution of the albacore along the coast from Mexico to Canada (Laurs, 1977) and this has proved of strategic value in the choice of location of the vessels prior to the opening of the season.

Brief details of the other four services are given after Tomczak (1977).

(3) For the Australian seasonal coastal fishery for southern bluefin, the product is a chart of schools of fish sighted and sea surface isotherms based on airborne radiometry from spotter aircraft.

(4) In the French northeast Atlantic albacore fishery, information on temperature, mainly from research and fishing vessels and aircraft, is used to produce charts of sea surface temperature. Predictions of sea state and weather from meteorological satellites, are also transmitted to the fishing fleet.

(5) In the Gulf of Guinea, airborne radiometry has been used on a limited time and space scale to assist in the forecasting of suitable fishing zones for surface yellowfin and skipjack.

(6) The Japanese Fisheries Environmental Information Services Center is well established and for some time has been providing a large variety of information in many formats to all segments of the Japanese fishing industry, both ashore and afloat. Support is provided for the seasonal coastal fisheries for albacore, skipjack, and bluefin through forecasts of temperature conditions, currents, marine weather, and also at the strategic level through advance predictions of long-term trends of abundance in certain pelagic fisheries such as skipjack.

The use of remote sensing techniques from aircraft in support of fisheries research was discussed in some detail by Stevenson & Pastula (1971) and Joseph & Stevenson (1974). In tuna fisheries the value lies in the use of airborne radiometry from spotter aircraft for detection of surface temperature fields, visual observations of current–water mass boundaries indicated by colour, slicks, weed lines, *etc*., as well as the sighting of tuna schools. Obviously these techniques are mainly limited to fisheries within range of land-based aircraft, *e.g*. coastal Australian southern bluefin fisheries. The authors listed above also speculated on the use of remote sensing of the ocean from spacecraft in support of fisheries and this subject was reviewed (for the entire marine science field) by Szekielda (1976). In particular, Joseph & Stevenson (1974) stressed the importance, especially for tuna, of information on sea surface temperature, water masses, currents, surface fronts, thermocline depth, and gradients. Such information concerning the thermocline can be derived from models involving sea surface temperature, wind intensity, direction and duration, and cloud cover.

Data derived from satellites dedicated to meteorology and oceanography, *e.g.*, United States GOES, NIMBUS, NOAA, TIROS series and European METEOSAT already are being used by the National Environmental Satellite Service, Office of Sea Grant, National Weather Service, and National Marine Fisheries Service on a routine basis in formulation of products for fisheries environmental services as well as in support of fisheries research projects. The future will certainly bring about an increasing use of available equipment and techniques to allow full use of infra-red, visible, and multispectral data to provide temperature and other oceanographic information mentioned in the preceding paragraph. Many problems relate to the processing of the remote sensing data from the various satellite sources (*e.g.*, uncertainties of radiation temperatures in the tropics; Barnett, 1977), acquisition of ground (sea) truth data, the subsequent integration with concurrently available data on the tuna fishery in question, and in some cases the method of transmission to the users (fishermen). In addition, especially in coastal upwelling zones, there may be problems because of persistent cloud cover and the transient nature of the oceanographic features. An understanding of the formation, movements, gradients, and persistence of fronts in relation to tuna distribution and abundance will probably be of the most immediate value to the tuna fishing industry. This probably means application at the scale of 1–100 km, and possibly up to the mesoscale of 100–1000 km. Of course, the real problem remains: that of finding a linkage mechanism between tuna and the environment. Remote sensing will probably serve in a supplementary manner in fishing industry operations; it has yet to be proved of value in management.

CONCLUDING REMARKS

It has been our purpose to review critically information on the apparent relationships between the tunas and their environment. What becomes evident from our review is essentially a detailed 'habitat description'. The next critical accomplishment by tuna researchers must be the gaining of an understanding of the dynamics of the tuna populations—their reproduction, rates of growth, migrations and concentrations, all of which are influenced by the dynamic and varying properties of the habitat. For instance, virtually nothing is known about how spawning success and subsequent year-class strength are affected by environmental factors. Such information should be included in the population dynamics models by which management is attempted. Nelson, Ingham & Schaaf (1977) indicated the importance of this in the case of the Atlantic menhaden (*Brevoortia tyrannus*). They were able to show that 84% of the variation from the Ricker spawner-recruit curve for the species was due to zonal Ekman transport, the mechanism by which larvae are transported from offshore spawning grounds to inshore nursery grounds. For the Pacific mackerel (*Scomber japonicus*) in the California Current, Parrish & MacCall (1978) dramatically demonstrated, through increased understanding of variations in recruitment, the informative and explicit value of including environmental factors in stock management models.

An understanding of the causal relations between environmental forcing processes and biological responses is important in designing an investigation of the effects of environment upon a species or stock. For example, Laurs *et al.* (1977) showed that the apparent relationship of North Pacific albacore to coastal upwelling fronts is, in fact, a response of the fish to the distribution of their forage, and not the thermal gradient itself. The forage, in turn, is responding to changes in plankton abundance associated with the front and not to the physical field. It may, however, be operationally easier to relate temperature and albacore than forage and albacore, in terms of management strategy, forecasting, or fishing operational considerations.

We expect that more work will be done, that our understanding will improve, and that managers of the fisheries resources and directors of fisheries research will increasingly recognize the rôle of the environment in the ecology of the fish and in the operation and management of the fisheries, and thus will be able to act with wisdom on behalf of both man and resource. It would be prudent now to test a number of the hypotheses that have been set forth. Some suggested areas of future investigation are enumerated briefly here.

(1) Many hypotheses about the effects of environmental variables in determining tuna occurrence have been put forward, but few have been adequately tested in the field. For instance, it has been argued that certain areas and water layers are suitable habitats for skipjack of only certain sizes because of temperatures and oxygen concentrations, but no adequate attempts to verify this proposition have been made. Also, the assumed relations between aggregations of tunas and their prey have not been verified sufficiently in the ocean. Such hypotheses should be tested in selected oceanic areas at appropriate periods. We recognize that field work in oceanic waters is expensive, but nevertheless, more of such work is needed. Furthermore, one should not overlook the fact that recent advances with multispectral visible and infrared sensors, and concomitant processing techniques give us the opportunity to use satellite remote sensing for comprehensive and synoptic monitoring of surface features and events over large ocean areas.

(2) The biological processes which have the greatest potential for elucidating cause and effect relationships with climatic factors are: (a) survival and growth of larval stages, and (b) predation. The breeding pattern for most species of tuna, and especially the more tropical ones, is to spawn large numbers of eggs throughout much of the year over large oceanic areas. By this tactic, adverse environmental conditions encountered by larvae and juveniles appear to be minimized and chances for survival enhanced. The larval period is short and growth is rapid, which further reduces adversity from environmental conditions, cannibalism, and predation. Thus, the Cushing & Dickson (1976) match–mismatch theory of spawning and environmental events should not become a major factor for survival. In the case of bluefin and southern bluefin tunas with relatively discrete spawning areas and short spawning seasons (see pp. 469–470) following long migrations, the match–mismatch theory may be more relevant. The early stages in the life history of tunas (larvae to juveniles) still probably are the most important with regard to the influence of environmental factors on survival and recruitment to fishable stocks. It is these early stages about which little is known concerning their distribution and abundance, physiology, behaviour, and general ecology. The requirements of young tunas also may determine

some features of the distribution of adult tunas. Studies should be intensified to fill this gap in our information even although development of new techniques and gear may be required.

(3) Indices of environmental phenomena that appear causally related to tunas should be specified and methods of measuring some of them (*e.g.* their food supply) should be improved. These should then be used to improve the basic data collected for scientific and management objectives. When a relationship is finally established between a tuna's distribution or behaviour and some aspect of its environment, useful short-term information for the fishery can be provided by monitoring those aspects, as is the case now with the environmental services mentioned earlier (pp. 500–503). Long-term forecasting, on the order of six months or more, would have greater value. This will not be possible, however, until much more is known of the processes and rates by which the important environmental features develop. Satellite remote sensing of oceanic conditions may prove to be valuable in this regard.

It behoves those interested in tuna forecasting to make their special interests better known to others in the oceanographic community, and to co-operate with them in the necessary work. It should not be overlooked that some marine scientists who were not formerly interested in fish populations are now becoming so, recognizing the rôle of those populations in ecosystem structure.

(4) Changes over time in size, integrity, and gene pool composition of tuna schools should be observed to learn the make-up of the basic school unit, how and under what circumstances the school grows and the dynamics of that growth, and how the school's composition (inter- and intraspecific) changes over time. Observations should also be made of any alteration of behaviour of the individuals in the school as the school size and structure change. In this respect, the theoretical study of Clark & Mangel (1979) on aggregation and fishery dynamics using schooling and the purse-seine tuna fisheries is of interest because of the implications for fisheries management.

(5) The hypotheses on migration and movement by 'active' and 'passive' means (Seckel, 1972; Williams, 1972) should be tested while being aware of the possibility that the two modes may each play a rôle to varying degrees, depending on the stage in the life history of the fish.

(6) Tunas should be tracked with acoustic tags to record their small-scale behaviour of movement. General patterns, if any, should be specified and attempts made to explain them in terms of contemporaneous environmental observations.

(7) Investigations of the methodology of defining tuna stocks, and of measuring changes in their condition over time should be continued.

(8) Additional information of many kinds is needed on many of the tuna species. For example, relatively little is known about the biology of bigeye tuna, even though it is a major, highly desired resource. In addition, some advances in fishing technology may be needed to exploit the relatively deep-dwelling adults of this species more effectively.

This general lack of knowledge is certainly true of many of the species at present of minor market value; *e.g. Auxis*, *Euthynnus*, *Sarda*, *Allothunnus*, *etc.* The frigate or bullet tunas of the genus *Auxis* are a worldwide under-utilized resource with a potential production of greater than one million metric tons (Gulland, 1971). Our overall knowledge of the biology of frigate tunas and relationships to their habitat is, however, still very weak (Uchida, in press) and their importance as major components of the food chain of apex predators such as other tunas, billfishes, and sharks is virtually unknown. In addition, the market demand, in terms of the global tuna industry, for this small, dark-meat tuna apparently is not large. This may not be the case, however, in the lesser developed nations of the world desirous mainly of increasing total available fish catch.

(9) Porpoise–tuna interactions should be observed under various environmental and behavioural conditions in order to develop explanations of why the porpoise–tuna association varies in strength between species and between years. Environmental conditions extant in these various circumstances should be monitored for possible influences of the environment on the association.

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EFFECT OF FEEDING HISTORY AND EGG SIZE ON THE MORPHOLOGY OF JACK MACKEREL, *TRACHURUS SYMMETRICUS*, LARVAE

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INTRODUCTION AND OBJECTIVES

Starvation of marine fish larvae after yolk absorption may be one of the principal causes of larval fish mortality (Hunter, 1976a). Past studies showed that starvation in fish larvae could be detected by using morphometric criteria (Arthur, 1976; Ehrlich et al., 1976; Nakai et al., 1969; Kostomarova, 1962), histological criteria (Ehrlich et al., 1976; O'Connell, 1976; Umeda and Ochiai, 1975), and chemical criteria (Ehrlich, 1974a, 1974b). Use of histological criteria has several advantages over use of morphometric and chemical criteria. Histological criteria describe condition of individual larvae, indicate early starvation, and are independent of size; the disadvantage is that histological analyses are time consuming. Although morphometric paramenters require less time, past studies (Arthur, 1976; Ehrlich et al., 1976; Nakai et al., 1969; Kostomarova, 1962) show that they were not sensitive enough to indicate early starvation or to estimate condition of individual larvae.

In a recent laboratory study, Theilacker (1978) identified early starvation in individual jack mackerel, *Trachurus symmetricus*, larvae using either histological or morphometric criteria by comparing starved larvae to those fed at a constant food density. Larvae in the ocean are subject to widely varying food concentrations including no food (Lasker, 1975); hence, wild larvae may grow at different rates and sizes of body parts may change at different rates. Thus, histological and morphometric characteristics are needed that assess condition of larvae with variable feeding histories.

The objective of this study was to develop a sensitive morphometric technique that identified individual larval condition and was independent of egg size and feeding history. To accomplish this, the condition of jack mackerel larvae reared in the laboratory was investigated when initial feeding was delayed or when food type or density varied. Also, because the size of jack mackerel eggs varied, the condition of fed and starved larvae from large and small eggs was compared. In addition, the rate of recovery of tissues degenerated from starvation (Theilacker, 1978) was determined.

METHODS

COLLECTING AND REARING

Jack mackerel eggs were collected 20–30 miles off the coast of San Diego, California, in June and July 1977, by towing a 1/2 m diameter net with a plastic cod end just below the sea surface. These jack mackerel eggs were smaller than those collected in the earlier study (Theilacker, 1978). Thus, to test for effect of egg size, results from Theilacker (1978) were used in this study.

The larvae were reared in 100-liter black circular tanks at 15.5° ± 0.1° C using rearing techniques described by Lasker et al. (1970), Theilacker and McMaster (1971), and Hunter (1976b). The foods used were rotifers, *Brachionus plicatilis*, (66 to 182 mμ wide; Theilacker and McMaster, 1971) and *Gymnodinium splendens*, a dinoflagellate (53 mμ diameter; Scura and Jerde, 1977). All rearing experiments were conducted with early, post-yolk-sac larvae of less than 4.0 mm standard length; wild jack mackerel at this size select prey between 50 and 200 mμ in width (Arthur, 1976).

Four feeding treatments were used: (1) high food density (50 *Gymnodinium* and 30–50 rotifers per ml) given at the time yolk is nearly absorbed and feeding begins, Day 5 (Group I, Table 1); (2) high food density

Table 1. Daily means of five body measurements of *Trachurus symmetricus* larvae subjected to various feeding treatments.

Small-egg larvae				Standard length (mm)		Head length (mm)		Eye diameter (mm)		Body depth at pectoral (mm)		Body depth at anus (mm)	
Treatment	Group	n	Day	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
Fed	I	11	6	3.318	.185	.703	.051	.267	.015	.430	.028	.198	.011
		14	7	3.318	.154	.737	.041	.277	.017	.441	.029	.192	.020
		15	8	3.360	.148	.749	.054	.278	.024	.448	.043	.201	.018
		11	9	3.450	.211	.825	.079	.303	.027	.519	.055	.213	.021
		5	10	3.520	.110	.877	.015	.333	.009	.554	.023	.235	.014
Feeding delayed one day	II	23	7[a]	3.285	.112	.718	.036	.267	.014	.403	.027	.191	.016
		38	8	3.243	.139	.739	.040	.276	.018	.436	.040	.191	.016
		29	9	3.317	.136	.767	.054	.284	.020	.445	.055	.202	.019
		15	10	3.290	.126	.785	.051	.291	.018	.477	.037	.202	.017
		5	11	3.390	.074	.831	.038	.316	0.33	.487	.052	.206	.013
		3	12	3.450	.229	.827	.052	.312	.026	.476	.071	.204	.017
Feeding delayed two days	III	19	8	3.147	.120	.721	.033	.268	.011	.423	.025	.196	.012
		22	9	3.173	.127	.749	.028	.274	.011	.430	.043	.185	.017
		10	10	3.140	.117	.751	.058	.270	.023	.462	.052	.190	.016
		2	11	3.050	.071	.774	.145	.293	.054	.501	.165	.191	.054
Starved	IV	28	6	3.248	.121	.687	.034	.251	.013	.390	.027	.185	.013
		6	7	3.075	.147	.663	.056	.249	.021	.368	.032	.173	.007
Large-egg larvae[b]													
Fed	V	14	6	3.375	.075	.704	.031	.252	.016	.458	.022	.208	.016
		15	7	3.483	.126	.736	.038	.259	.014	.476	.031	.204	.016
		15	8	3.560	.132	.770	.030	.286	.015	.519	.040	.218	.016
		10	9	3.826	.237	.845	.056	.316	.020	.590	.039	.250	.013
		15	10	3.717	.203	.851	.074	.306	.029	.576	.061	.235	.022
Starved	VI	14	6	3.311	.109	.655	.036	.236	.016	.413	.032	.179	.016
		15	7	3.355	.131	.688	.020	.248	.013	.417	.023	.183	.012
	VII	19	8	3.041	.175	.646	.035	.232	.014	.419	.025	.174	.015
Small-egg-larvae[c]													
High-low density	VIII	11	6	3.186	.092	.657	.027	.244	.009	.405	.023	.167	.010
		15	7	3.190	.171	.702	.036	.271	.010	.418	.033	.194	.013
		14	8	3.257	.160	.714	.024	.270	.017	.414	.041	.183	.017
		11	9	3.082	.261	.680	.059	.270	.019	.423	.041	.185	.016
		2	10	3.025	.318	.731	.024	.281	.012	.425	.024	.187	.024
Fed wild plankton	IX[d]	5	6	3.360	.152	.717	.052	.269	.008	.435	.015	.197	.015
		5	7	3.280	.277	.700	.066	.265	.019	.445	.035	.190	.014
		6	8	3.383	.133	.793	.051	.289	.022	.456	.036	.210	.009
		8	9	3.450	.160	.814	.052	.291	.021	.459	.030	.210	.018
		6	10	3.617	.216	.861	.085	.315	.030	.558	.073	.232	.026
		5	11	3.510	.074	.870	.046	.320	.019	.530	.039	.224	.019

[a] Day 7, Group II larvae were not included in morphometric SWDA (see text).

[b] Data from Theilacker (1978). Days 8, 9 and 10, Group V larvae are not included in morphometric SWDA. Size class selected for SWDA = 3.0–3.5 mm.

[c] Condition of larvae in Treatments VIII and IX was compared by morphometric and histological analyses; treatments were not included in morphometric SWDA.

[d] Larvae reared by Kim Devonald, Scripps Institution of Oceanography.

beginning on the day after yolk absorption, Day 6 (Group II); (3) high food density beginning 2 days after yolk absorption, Day 7 (Group III); (4) no food (Group IV). Measurements of larvae sampled from these four treatments were used to develop the morphometric criteria that identify larval fish condition.

Beginning on day six, 5–30 larvae were sampled daily and preserved in Bouin's fixative. After preservation, the standard length (SL, tip of upper jaw to perpendicular at end of notochord), head length (HL, tip of upper jaw to cleithrum), eye diameter (ed), body depth at the pectoral (bd-1), and body depth at the anus (bd-2) were measured. After measurement larvae were prepared for histological examination using standard techniques (Theilacker, 1978).

MORPHOMETRIC ANALYSIS

Morphometric analysis of larval fish condition was based on a stepwise discriminant analysis (SWDA). This technique finds the best set of variables (body measurements) that discriminate satisfactorily between known groups of larvae; by using the variable set, this technique predicts the group to which the individual larvae appear to belong. A known group in this study usually means a group of animals pooled by treatment (Table 1); however, there was one exception, Group II, that is explained in Results. The variables (body measurements) in which the feeding and starving groups were expected to differ were: (1) HL; (2) ed; (3) bd-1; (4) bd-2; (5) HL/SL; (6) ed/SL; (7) bd-1/SL; (8) bd-2/SL; (9) ed/HL; (10) bd-1/HL; (11) bd-2/HL. To classify individual larval condition all 11 variables were entered into the SWDA.

Larvae of between 3.0 and 3.5 mm standard length were selected for morphometric SWDA.

HISTOLOGICAL ANALYSIS

Condition ("healthy", "recovering", "intermediate", or "starved") of all larvae in each treatment was determined by examining the histological characteristics of the pancreas, liver, and gut (Theilacker, 1978).

Because the SWDA selects discriminating variables (larval body measurements) based on all cases within a group, it was desirable that most larvae within each group have similar nutritional conditions, i.e., have the same histological grade. Therefore, for the SWDA all larvae were not retained in Group II (see Results). The dominant histological condition of the larvae within each group (feeding treatment) was used to define the group.

RESULTS

GROWTH

Jack mackerel eggs collected for this study were 0.90 ± 0.03 mm live diameter ($n = 32$) and larvae hatched at 2.1 ± 0.05 mm live SL ($n = 20$). These eggs were 0.08 to 0.10 mm smaller than eggs collected in an earlier study (Theilacker, 1978), the results of which are used in this study. During a 4-day period after the first day of feeding, fed larvae (Group I, Table 1) grew at 0.051 mm/day and 1-day delay-fed larvae (Group II) grew at 0.026 mm/day (Fig. 1). Larvae that were starved 2 days before feeding (Group III) did not grow over the 4-day experiment.

The relationship between body depth and standard length was similar between larvae fed continuously on rotifers and larvae fed rotifers for two or more days following 1-day delay in feeding. This relationship held only for larvae of the same length but not for those of the same age (Groups I and II, Table 1). Starved larvae were usually smaller than unstarved larvae of the same age.

HISTOLOGICAL ASSESSMENT OF LARVAL GROUPS

In many of the larvae given food, histological evidence existed for both feeding and starving. In these larvae the liver, pancreas, and gut tissues appeared normal and there were inclusions in the hindgut that indicate digestion; however, there were also separations between midgut mucosal cells, indicating the larvae had starved at some time.

This condition was between the histological conditions defined in the earlier study of large-egg larvae (Theilacker, 1978) as "healthy" (feeding larvae) and "intermediate" (early-starved larvae, usually larvae that starved 1 or 2 days). In discussions of larval fish histology that follow, reference to this condition is "recovering". "Recovering" larvae are eating and digesting food but have starved at some time.

In "recovering" larvae that were starved 2 days before feeding, vacuoles were visible within the midgut cells. The appearance of these large vacuoles was unusual, and it suggests that the gut epithelium may be a site for intracellular digestion (Iwai, 1968) or storage. The liver cells of these larvae also had very large

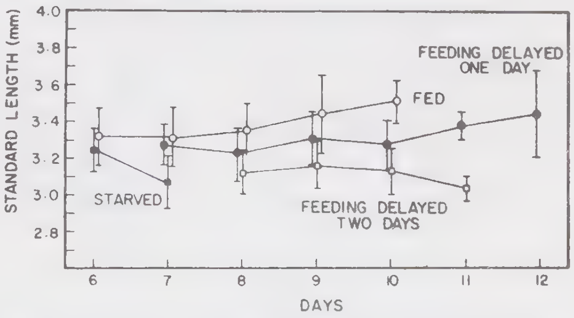

Figure 1. Growth of small-egg *Trachurus symmetricus* larvae with means and standard deviations. Feeding treatments are indicated, and sample size is in Table 1.

intracellalar spaces, probably areas for storage of glycogen. Both the condition in the midgut and the liver were unique to larvae feeding after 2 days of starvation.

The dominant histological condition of larvae within a group (I–VIII, Table 1) was used to define group condition (Fig. 2A). For Group I, continuously fed larvae, 76% were graded histologically as "healthy". However, some larvae given food did not eat; 7% of the larvae in Group I were starving and graded "intermediate" and 17% of the larvae were graded "recovering", i.e. larvae were eating but had starved at some time. Hence, 93% of the larvae belonging to Group I were eating. In Group II, tissue degeneration caused by 1 day of starvation had completely regenerated in 48% of the larvae that ate for 1 day and in 89% of the larvae after eating 2 days. Because at least 2 days of feeding were required before most larvae were "healthy", only larvae that fed 2 or more days after 1 day of starvation were included in Group II for the morphometric SWDA. As a result, 75% of Group II larvae were "healthy" and 20% were "recovering", therefore, 95% were eating. Tissue regeneration was never complete in larvae that fed 1–4 days after 2 days of starvation (Group III), 54% of the larvae were "recovering" and 44% were "intermediate". Therefore, about half of these larvae were eating and half were starving; no single histological condition dominated. For Group IV, larvae that were starved 1 or 2 days (early-starved), the majority, 78% received the "intermediate" grade and 19% were graded "starved", hence 97% were starving.

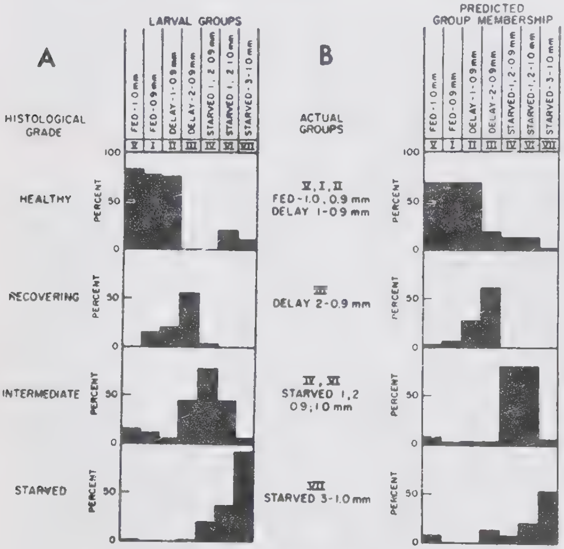

Figure 2. Comparison of larval classification by histological and morphological methods. (A) Using histological methods, larvae in each feeding treatment were divided into "Healthy", and "Reccovering", "Intermediate", and "Starved" categories. (B) Using morphometric methods, larvae were matched to their feeding treatment. The distribution of larvae was similar to histological groupings although the categories into which they are distributed are not exactly parallel, see text.

To simulate field conditions, both larvae from large and small egg groups were included in the morphometric SWDA (Fig. 2A) because egg size in the sea is unknown. The dominant histological condition of larvae hatching from large eggs (Theilacker, 1978) was as follows: fed larvae in Group V (Table 1), 85% "healthy", larvae starved 1 and 2 days (early-starved) in Group VI, 44% "intermediate" and 37% "starved" (hence 81% starving), larvae starved 3 days (late-starved) in Group VIII, 80% "starved" and 7% "intermediate" (hence, 87% starving).

MORPHOMETRIC SWDA

The SWDA was run with the same larval groups, I–VII (Table 1) used for histological analysis. Eleven morphometric variables (see Morphometric Analysis)

Table 2. Morphological classification of *Trachurus symmetricus* larvae. The number of larvae in the actual, predetermined group is compared with the predicted group membership determined by the stepwise discriminant analysis.

Actual group	Treatment	Egg size (mm)	n	Predicted group membership						
				V	I	II	III	IV	VI	VII
V	Fed[a]	1.00	26.	23	2	0	0	0	1	0
I	Fed	0.90	46.	1	20	11	3	4	5	2
II	Feeding delayed[b]	0.90	86.	2	23	26	26	9	0	0
III	Feeding delayed[c]	0.90	52	1	3	14	31	2	0	1
IV	Starved; 1 and 2 days	0.90	32.	0	0	2	2	20	6	2
VI	Starved; 1 and 2 days[a]	1.00	29.	4	1	0	0	6	17	1
VII	Starved 3 days[a]	1.00	15.	1	0	0	2	1	3	8

[a] Data from Theilacker (1978).

[b] Feeding delayed 1 day. Includes larvae fed 2 or more days after 1 day of starvation (see text).

[c] Feeding delayed 2 days.

were entered into the SWDA. The analysis selected a set of seven variables as the best set to discriminate between the predetermined groups. The variable set, listed in order of selection, was: (1) HL/SL; (2) HL; (3) bd-1/HL; (4) ed; (5) bd-2/HL; (6) bd-1; and (7) bd-1/SL.

The SWDA (Table 2) allowed differentiation between fed and starved larvae that hatched from large and small eggs, in particular Groups V vs. I and Groups VI vs. IV. SWDA classified larvae hatching from small eggs as belonging not only to their own feeding treatment but to several treatments; classification of larvae hatching from large eggs was more precise (Table 2).

COMPARISON OF HISTOLOGICAL AND MORPHOLOGICAL METHODS

The distribution of larvae to feeding treatment by SWDA was similar to that based on histological criteria (Fig. 2), although the four categories into which they are distributed are not exactly parallel. For example, all "healthy" larvae (first category, Fig. 2A) were reared in feeding treatments V, I, and II (with several exceptions for larvae hatching from large eggs), however, all larvae in treatments V, I, and II (first category, Fig. 2B) were not "healthy" — some larvae given food did not eat. In Results (Histological Assessment of Larval Groups), feeding treatments V, I, and II were called "healthy" treatments, i.e., the majority of the larvae reared with these treatments were "healthy". Even though it is not accurate to compare the histological and morphological distributions of larvae as shown in Figure 2A vs. 2B, the comparison does allow a relative assessment of the sensitivity of the SWDA.

The SWDA assigned a reasonable proportion of larvae to correct feeding treatment. To summarize Figure 2, 77% of the larvae belonging to three feeding groups, Groups V, I, and II, were histologically graded "healthy"; the SWDA matched 66% of the larvae taken from Groups V, I, and II correctly to their feeding treatment. For larvae that were starved 1, 2 or 3 days, Groups IV, VI, and VII, 89% received the starved histological grades ("intermediate" and "starved"); the SWDA matched 84% of the starved larvae taken from Groups IV, VI, and VII correctly to their feeding treatment.

EVALUATION OF MORPHOMETRIC SWDA AS A CLASSIFICATION TECHNIQUE

The discriminant analysis, SWDA, can now be used as a classification technique since a set of variables, combination of body measurements, has been found that satisfactorily discriminates larvae with known feeding histories. To test the power of the SWDA as a classification technique, a discrimination function derived from the variable set was used to classify condition of larvae with "unknown" feeding histories. In this application of SWDA the independent variables were not selected but entered directly into the analysis. To evaluate the accuracy of this test, all larvae were examined histologically.

Two groups of larvae, reared in experiments where food density and type were varied, were treated as the "unknown" sampled. The treatments for the two groups of larvae that hatched from small eggs were: (1) high-low rotifer density, 30–50/ml given on first day of feeding and 6–12/ml for the next 5 days and temperature at 15.5° C (Group VIII, Table 1); and (2) wild plankton diet of one copepod/ml, nauplius or copepodite 80–200 mμ width, given at time of first feeding and temperature at 17° C (Group IX, Table 1).

Larvae fed rotifers at high-low densities, Group VIII, grew at 0.036 mm/day for 2 days and then began to shrink after the rotifer density was decreased (Fig. 3). In contrast, larvae fed wild plankton at low densities, Group IX, grew at 0.064 mm/day (Fig. 3), about the same rate as larvae fed rotifers at high densities, Group 1, (Fig. 1).

All larvae sampled from both "unknown" groups, Groups VIII and IX (Table 1), were retained for the SWDA classification. Size range for larvae fed rotifers at high-low density, Group VIII, was 2.7–3.5 mm. Larvae fed wild plankton at low density, Group IX, were larger, 3.0–3.8 mm (Table 1), and in better condition (Table 3) than larvae fed rotifers at low density, Group VIII.

Table 3 compares the use of histological and morphometric criteria to classify individual larvae. For the wild plankton treatment, SWDA classified 28 larvae as belonging to the three feeding groups labelled as "healthy", Groups V, I, and II (see Histological

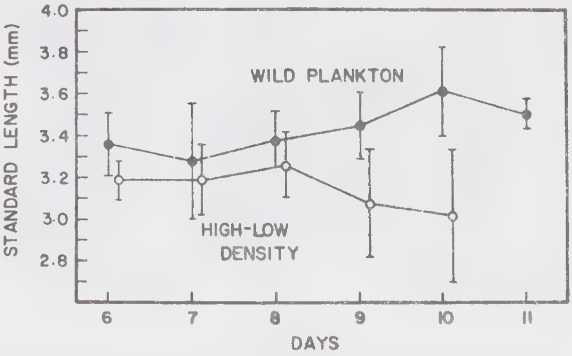

Figure 3. Growth of small-egg *Trachurus symmetricus* larvae with means and standard deviations. Feeding treatments are indicated, and sample size is in Table 1.

Table 3. Small-egg *Trachurus symmetricus* larvae were fed wild plankton at a low density (Group IX) or a varied density of rotifers (Group VIII). Each larva in both treatments was classified with the morphometric SWDA and the histological method. Larvae classified incorrectly with the SWDA are underlined. Total number of larvae within each experiment does not agree with Table 1, as several larvae were lost during the microtechnique procedure.

	Morphometric classification and predicted group membership						
Histological grade	Fed 1.0 mm V	Fed 0.9 mm I	Delay 1 day 0.9 mm II	Delay 2 day 0.9 mm III	Starved 1 and 2 days 0.9 mm IV	Starved 1 and 2 days 1.0 mm VI	Starved 3 days 1.0 mm VII
Plankton Treatment							
Healthy	3	10	7	0	0	0	1
Recovering	1	0	3	0	1	0	1
Intermediate	0	2	2	1	0	0	0
Starved	0	0	0	0	0	0	0
Density Treatment							
Healthy	0	3	1	0	0	0	0
Recovering	1	7	4	5	6	0	1
Intermediate	0	0	1	1	7	6	3
Starved	0	0	0	0	2	0	1

Assessment of Larval Groups), 20 of these larvae, 71% were histologically graded "healthy" and four were graded "recovering" (Table 3). A "recovering" larva had eaten and was digesting food; the SWDA classification of these four larvae into the "healthy" groups was not unreasonable. Twenty-four of the 28 larvae, 86%, identified as belonging to the "healthy" groups by SWDA were identified as eating by histology. SWDA predicted that three larvae were starving; these larvae were classified as belonging to the three starving groups, Groups IV, VI, and VII. These allocations were incorrect; histologically there were no starving larvae.

In the high-low rotifer density treatment, SWDA classified 17 larvae as belonging to the three "healthy" feeding groups, Groups V, I, and II, four of these larvae received the "healthy" histological grade and 12 were graded "recovering". Therefore, 94% of the larvae classified by SWDA as belonging to a feeding group were eating. SWDA classified 26 larvae into the three starving groups, Groups IV, VI, and VII, nineteen, 73%, of these larvae received the "starving" histological grades ("intermediate" and "starved").

The SWDA classifications in Table 3 that were unreasonable are underlined. In sum, 88% of morphometric SWDA classifications of larvae to feeding treatments were reasonable, as verified by a histological examination of all larvae.

DISCUSSION

The purpose of these experiments was to document a morphological method that can be used to identify probable feeding condition of field-collected larvae. Analysis of early, post yolk-sac jack mackerel larvae reared in the laboratory with various feeding regimes showed that larvae of the same size which were "healthy" according to histological analysis can differ in other body measurements and age. It was found that body proportions differed between larvae of the same size that hatched from large (Theilacker, 1978) and small eggs. For example, body depth of fed small-egg larvae was deeper than fed large-egg larvae of the same size, though this relationship did not hold when larvae were the same age (Table 1). Growth rate of larval body parts may vary because larvae hatched from different size eggs or because larvae experienced different feeding conditions.

Growth and condition of jack mackerel hatched from small eggs were assessed in this study for a variety of feeding treatments. Small-egg larvae, fed either high rotifer densities or low copepod densities, grew at about the same rate and were "healthy", but larvae fed a low density of rotifers grew more slowly and were in poor condition. Therefore, at low densities, the quality of copepods as a food for larval jack mackerel was superior to rotifers. When fed at high rotifer densities, growth rate of small-egg larvae was less than the growth rate of large-egg larvae (Fig. 4).

In general, egg size appears to be an important factor that affects resistance to starvation and influences growth (Ware, 1975). In the jack mackerel experiments, large-egg larvae starved more slowly and lived 1 day longer without food (Theilacker, 1978) than small-egg larvae (Fig. 4). These results agree with studies by Blaxter and Hempel (1963) on herring, and Stanley (1977), however collected conflicting data, indicating that there was no influence of egg size on

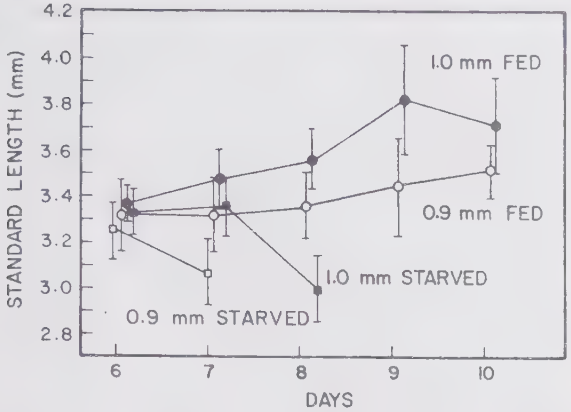

Figure 4. Comparison of fed and starved, large- and small-egg *Trachurus symmetricus* larvae with means and standard deviations. Sample size is in Table 1. Data for large-egg larvae from Theilacker (1978); data for small-egg larvae is the same as in Figure 1.

survival time during starvation for Japanese medaka, *Oryzias latipes*. Blaxter and Hempel (1963) also found that, with a large difference in herring egg size, the duration of the yolk-sac stage differed. This was not the case with jack mackerel, the difference in egg size was small and the time from hatching to first feeding was the same, 5 days at 15.0° to 15.5° C.

Both large- and small-egg jack mackerel larvae, which were starved for 1 and 2 days after yolk absorption, ate immediately after the addition of food. This behavior was similar to most other fish larvae (Hunter, in press). A 1-day period of starvation preceding the feeding of larvae from small eggs slowed the onset of growth. Growth did not proceed until the internal tissues that had deteriorated during starvation, had recovered. The energy for growth may have been diverted to tissue repair. In larvae starved for 2 days before feeding, evidence of cellular deterioration in the gut, pancreas and liver remained after feeding commenced. About half of these larvae appeared to be storing or digesting material in the gut epithelium. Although the larvae were feeding and "recovering" after 2 days of starvation, there was no growth during the experiments. These findings differ from results of May (1971) He found that grunion, *Leuresthes tenuis*, larvae were extremely resistant to starvation and that growth of larvae proceeded at the same rate when starved up to 16 days before feeding.

Evidence of morphometric differences between laboratory-reared and sea-collected larvae indicate that it may be difficult to transfer laboratory-collected data to the sea (Blaxter, 1975). Most data substantiating this hypothesis were collected during long-term laboratory experiments. An attempt was made to avoid this objection by restricting (1) the time of my experiment to 5 days; and (2) the size class selected for SWDA analysis to 3.0–3.5 mm SL.

Recently developed morphological criteria that identify larval fish condition were applied in this study. It was expected that complex relationships in larval fish morphology would occur between larvae fed at various food densities, including no food, delayed initial feeding, and between feeding and starving larvae that had hatched from different egg sizes. However, by using a combination of several larval fish body measurements, the SWDA, it was possible to correctly assign most larvae into feeding groups; allocations were corroborated by a histological examination of individual fish. Morphological criteria for assessment of condition of wild larvae are most useful than histological criteria because they take much less time to determine, cost less, and can be used routinely. The morphometric technique should allow reasonable estimates — independent of egg size and feeding history — of condition of early, post yolk-sac wild larvae. These estimates may be useful for detecting the incidence of starvation in sea-caught larvae and for predicting larval survival in the field.

SUMMARY

Because starvation of marine fish larvae after yolk absorption may be an important factor influencing larval survival, there is a need to recognize starvation in wild larvae. The primary purpose of this study was to develop morphometric criteria sensitive enough to identify condition of larvae that hatched from large and small eggs and were subjected to varying feeding treatments. Morphometric criteria for assessing larval condition are not as precise as histological criteria; however, morphometric criteria are more useful than histological criteria because they take less time to determine (measuring body parts is relatively easy) and therefore could be used routinely in analyses of wild larvae.

In this study a multivariate statistical analysis (SWDA) was used to assess the condition of jack mackerel larvae. The criteria used in the analysis were based on measurements of larvae hatched from large and small eggs and raised under conditions in which availability of food and time of feeding (delayed by 1 or 2 days) were varied. The larvae were divided into seven groups, according to their feeding treatment and egg size. Using the SWDA, larvae were classified in each controlled feeding group according to probable feeding history. All larvae in the seven groups were examined histologically to assess the power of the morphometric technique to properly classify condi-

tion of individual larvae. The histological analysis graded 77% of the larvae belonging to three feeding groups as "healthy" and SWDA matched 66% of the larvae taken from these feeding groups correctly. In the three starving groups, 89% received the histological "starved" grades and SWDA matched 84% of the starved larvae correctly to the three starved treatments. Hence, SWDA assigned a reasonable proportion of larvae to correct feeding treatment. Classification of larvae by SWDA was more precise for larvae hatching from large eggs than for larvae hatching from small eggs.

Histological analysis of larvae showed that tissue degeneration caused by 1 day of starvation after yolk absorption completely regenerated in 89% of the larvae after feeding for 2 days. However, the 1-day period of starvation slowed the onset of growth. Tissues never completely regenerated in feeding larvae following 2 days of starvation after yolk absorption.

Growth rate of larval body parts was found to vary because larvae hatched from different size eggs or because larvae experienced different feeding conditions. Resistance to starvation was 1 day longer for larvae hatching from large eggs than for larvae hatching from small eggs.

To test the sensitivity of the morphometric criteria selected by SWDA, SWDA criteria were used to classify condition of larvae raised in two independent experiments in which type of food (wild vs. laboratory cultured) and density of food were varied. SWDA classification of each larva was evaluated by examining each larva histologically. Eighty-eight percent of the larvae raised in independent experiments had similar condition classifications by SWDA method and histological method. It was concluded that the morphometric method should allow reasonable estimates — independent of egg size and feeding history — of condition of early, post yolk-sac wild larvae.

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AGE AND GROWTH OF SKIPJACK TUNA, *KATSUWONUS PELAMIS*, AND YELLOWFIN TUNA, *THUNNUS ALBACARES*, AS INDICATED BY DAILY GROWTH INCREMENTS OF SAGITTAE

James H. Uchiyama[1] and Paul Struhsaker[2]

ABSTRACT

Counts of the daily growth increments on otoliths provided the means for establishing growth curves for central Pacific skipjack tuna, *Katsuwonus pelamis*, up to 3 years old and for central Pacific yellowfin tuna, *Thunnus albacares*, up to 2 years old. The data indicated three stanzas of linear growth for 51 skipjack tuna ranging in size from 3 to 80 cm fork length. Estimated daily growth rates were 1.6 mm/day for fish up to a length of about 27.0 cm; 0.8 mm/day for fish between 27.0 and 71.4 cm; and 0.3 mm/day for fish between 71.4 and 80.3 cm. Growth data for 20 eastern Pacific skipjack tuna ranging in size from 38 to 65 cm fork length suggested that skipjack tuna in the eastern Pacific grew at a slower rate than those from the central Pacific.

Age determinations of 14 central Pacific yellowfin tuna suggested possibly two stanzas of linear growth. Estimated growth rates are 1.4 mm/day for fish up to a length of 64.2 cm and 0.9 mm/day for fish between 64.2 and 93.0 cm. Growth curves from this study were compared with published growth curves based on other methods.

The validity of daily growth increments was tentatively determined by observations on skipjack and yellowfin tunas held in captivity. Agreement of our growth curves with those of previous studies on the same stock of tunas using other growth estimating techniques also suggests that our aging technique is acceptable. However, the day-to-growth increment relation and the effect of various variables on the formation of growth increments of tunas need to be investigated further.

The many studies on age and growth of skipjack tuna, *Katsuwonus pelamis*, have primarily utilized three basic methods. Brock (1954), Schaefer (1961), Kawasaki (1965), Joseph and Calkins (1969), Yoshida (1971), Marcille and Stequert (1976a), and Diaz[3] determined growth rate and estimated the age of skipjack tuna by examining modal progression in length-frequency distributions. Yamashita and Waldron (1959), Shaefer et al. (1961), Clemens and Roedel (1964), Rothschild (1967), and Joseph and Calkins (1969) used data from tagged skipjack tuna to determine growth rates. Wild and Foreman (1980) estimated the growth rate of eastern Pacific skipjack tuna from the recapture fork length, the known period of growth, and the linear change in an otolith dimension following a tetracycline injection which was used to estimate length at marking. Marks on hard parts such as vertebrae and dorsal spines were interpreted to determine age and growth of skipjack tuna by Aikawa and Kato (1938), Yokota et al. (1961), Shabotiniets (1968), Batts (1972), and Chi and Yang (1973). Numerous reviews have been written on the subject and the lack of agreement on the aging and growth rate of skipjack tuna has frequently been noted.

Likewise, many studies have been conducted on age and growth of yellowfin tuna, *Thunnus albacares*. Moore (1951), Yabuta and Yukinawa (1957), Hennemuth (1961), Davidoff (1963), Diaz (1963), Le Guen et al. (1969), Yang et al. (1969), Le Guen and Sakagawa (1973), and Marcille and Stequert (1976b) have estimated age and growth rate by the analysis of modal progression in either length or weight frequencies. Blunt and Messersmith (1960), Schafer et al. (1961), and Bayliff[4] used results of their tagging experiments to determine the growth rate of yellowfin tuna in the eastern Pacific. Wild and Foreman (1980) estimated the growth rate of eastern Pacific yellowfin tuna by

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[3] Diaz, E. L. 1966. Growth of skipjack tuna, *Katsuwonus pelamis*, in the eastern Pacific Ocean. Unpubl. rep., 18 p. Inter-Am. Trop. Tuna Comm., La Jolla, Calif.

[4] Bayliff, W. H. 1973. Observations on the growth of yellowfin tuna in the eastern Pacific Ocean derived from tagging experiments. Unpubl. rep., 26 p. Inter-Am. Trop. Tuna Comm., La Jolla, Calif.

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their tetracycline-otolith method. Aikawa and Kato (1938), Nose et al. (1957), Yabuta et al. (1960), Tan et al. (1965), and Shabotiniets (1968) interpreted marks on scales, dorsal spines, and the centrum of vertebrae to estimate age and growth. These studies were performed on commercial-sized fish (>2 kg); growth during early life (<2 kg) has yet to be examined.

Pannella's reports (1971, 1974) provided circumstantial evidence that the smallest discernible growth increments in the sagittae (otoliths) of fish are deposited daily. More recent studies provide direct evidence that these growth increments are diel phenomena in sagittae of temperate (Brothers et al. 1976; Taubert and Coble 1977; Barkman 1978) and tropical (Struhsaker and Uchiyama 1976; Wild and Foreman 1980) species of teleosts. In the study of the short-lived engraulid *Stolephorus purpureus*, the information gained from the reading of sagittae was utilized in the construction of a growth curve for the first 190 d after yolk-sac absorption (full life cycle) (Struhsaker and Uchiyama 1976). In the present paper, growth curves are presented for central Pacific skipjack tuna to an age of about 3 yr, based on a sample of 51 fish, and for yellowfin tuna to about 2 yr, based on 14 fish. Counts on sagittae from 20 skipjack tuna from the eastern Pacific and 5 skipjack tuna from Papua New Guinea are also given. The results are discussed in relation to earlier age and growth studies of these species.

METHODS

Otolith Preparation and Counting

The central Pacific skipjack and yellowfin tunas were caught in the vicinity of the Line Islands and Hawaii. All specimens >20 cm FL (fork length) are samples taken from commercial fisheries or caught by trolling. Specimens <20 cm FL are from stomach contents of troll-caught skipjack tuna and regurgitations of a seabird, *Sula* sp., after it landed on the deck of a research vessel.

Juvenile skipjack tuna from stomach contents were identified by vertebral counts and skeletal characters given by Godsil and Byers (1944) and Gibbs and Collette (1967). In one case, only the anterior portion of a juvenile skipjack tuna was collected; standard length (SL) was estimated from the length of the precaudal vertebrae using the equation given by Yoshida (1971). A small (7.0 cm FL) yellowfin tuna specimen was tentatively identified on the basis of skeletal characters given by Matsumoto et al. (1972) and descriptions of *Thunnus* livers by Godsil and Byers (1944) and Gibbs and Collette (1967).

The caudal rays were missing from most tuna specimens collected from stomachs. Fork lengths were estimated by increasing standard lengths by 3.3% (Matsumoto[5]).

Heads from which the sagittae were not immediately removed after collection were frozen or preserved in 75% isopropanol.

In tunas <100 cm FL, we obtained the sagittae by splitting or cutting the skull along the sagittal plane and teasing them from the semicircular canals. With experience, the cut could be made without damaging either of the sagittae. We cleaned the sagittae by teasing or brushing off the sacculus and nerve endings. Sagittae that were not mounted immediately were stored in distilled water or 40% isopropanol, but were then mounted within a year.

After removal and cleaning, sagittae from tunas >45 cm FL were etched in a 1% solution of HCl for 3-5 min. The otoliths were then rinsed with several changes of water, mounted in Euparal,[6] and, in most cases, permitted to clear for 4 wk or more. Short lengths of monofilament line prevented contact of the otolith with the glass cover slip.

Increment counts were made from the core,[7] the center of the nucleus, to the tips of the rostrum, antirostrum, and postrostrum (terminology of Messieh 1972) for most sagittae. On sagittae from fish >60 cm FL, counts were made only to the rostrum and postrostrum. When the edge of the rostrum and postrostrum was fringed with irregular projections, counts were made on the projections leading to the point. Specimens were examined at magnifications of 200-800×. A microscope with a zoom feature was found to be useful, as the width of daily increments varied.

Counting increments in whole mounted otoliths becomes progressively more difficult with increasing specimen size. Experience is best obtained by beginning with otoliths from young fish and progressing through older fish. The initial counts enable the investigator to determine the best path to follow from the core to the edge of the otolith. Eventually, the counts either converge on a value or repeated identical counts are obtained. The number of counts required to determine age is dependent on the readability of the otolith. An average of about 20 counts was made for fish >1 yr old. We found that yellowfin tuna sagittae were easier to read than those of skipjack tuna. In yellowfin tuna, the increments are wider and can be examined at a lower magnification (200×), which provides a broader view and greater depth of field. The increment counts on 15 skipjack tuna and 3 yellowfin tuna sagittae were verified by a second reader whose counts were within 9% (5.4% average deviation) of the original counts except for one which was 17% off the original count.

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[5] W. M. Matsumoto, Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96812, pers. commun. October 1974.

[6] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[7] Terminology agreed upon at the Otolith Workshop, Scripps Institution of Oceanography and Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, Calif., 12-16 July 1976.

Statistical Analysis

The parameters of linear growth stanzas were determined by the use of LINFIT, a computer program (Kamer[8]) which used the ordinary least squares procedure to fit two or three straight lines to bivariate data. Join points, also known as break points, are the places where one regime ends and another begins; these are assumed to exist. The range of the explanatory variable in which the join points are expected to occur must be designated. Given the range for these join points, the program performs the ordinary least squares procedure on each possible combination of regimes. The resulting output indicates the partitioning scheme, the intercept and slope of each fitted line representing a regime, the residual sum of squares for each regime, the combined residual sum of squares for the model, and the values of the dependent and explanatory variables at the join points. The linear growth stanzas used in this paper were selected under the following conditions: 1) minimized combined residual sum of squares for the model and 2) each join point associated with a partitioning scheme has a value for the explanatory variable which lies between the last data value in the regime to the left and the first data value in the regime to its right.

On the assumption that the maximum number of increments approximates the age of the fish in days, we calculated a growth curve for central Pacific skipjack tuna, eastern Pacific skipjack tuna, and central Pacific yellowfin tuna for comparison with other studies. The von Bertalanffy growth parameters were estimated on an annual basis using the computer program BGC3 (Abramson 1971).

ESTABLISHING THE GROWTH INCREMENT-DAY RELATION

The only direct evidence we have that a number of growth increments equal the same number of days came from the serendipitous opportunity to examine skipjack and yellowfin tunas under known captive conditions. These fishes were not held under strict experimental conditions and their primary use was not for aging studies; however, a detailed record on the amount of food consumed by each fish during the experiment was maintained. The experiment was similar to that used for nehu, *S. purpureus* (Struhsaker and Uchiyama 1976), and was carried out at the Kewalo Research Facility of the Honolulu Laboratory.

The stress of being hooked, transported, and confined in the community tanks at the Kewalo Research Facility, as well as the taking of little or no food during the first week of captivity, probably all contributed to the formation of a check mark on the otolith (Figure 1a, b). When the tuna were sufficiently recovered to feed normally, they received a daily ration which apparently was adequate to maintain life but inadequate for normal increment formation. Perhaps very thin increments were formed during this period, which might have added prominence to the check mark. When these tunas were fed to satiation throughout the day, the widths of the increments increased and became countable.

Under low magnification (200×), growth increments formed on the edge of a sagitta during the experiment were not as well defined as those of a tuna captured in the wild. The increments appeared thinner than normal when examined under high magnification (400×). For this reason, a sagitta was first examined under low power (200×) to locate the check mark and then examined under high power (400×) to enumerate the growth increments formed during the experimental feeding period. Although growth increments occurred all along the periphery of the sagitta, the full array of increments corresponding

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[8] Kamer, G. A computer program for fitting straight lines to regimented data. Manuscr. in prep. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, Hawaii.

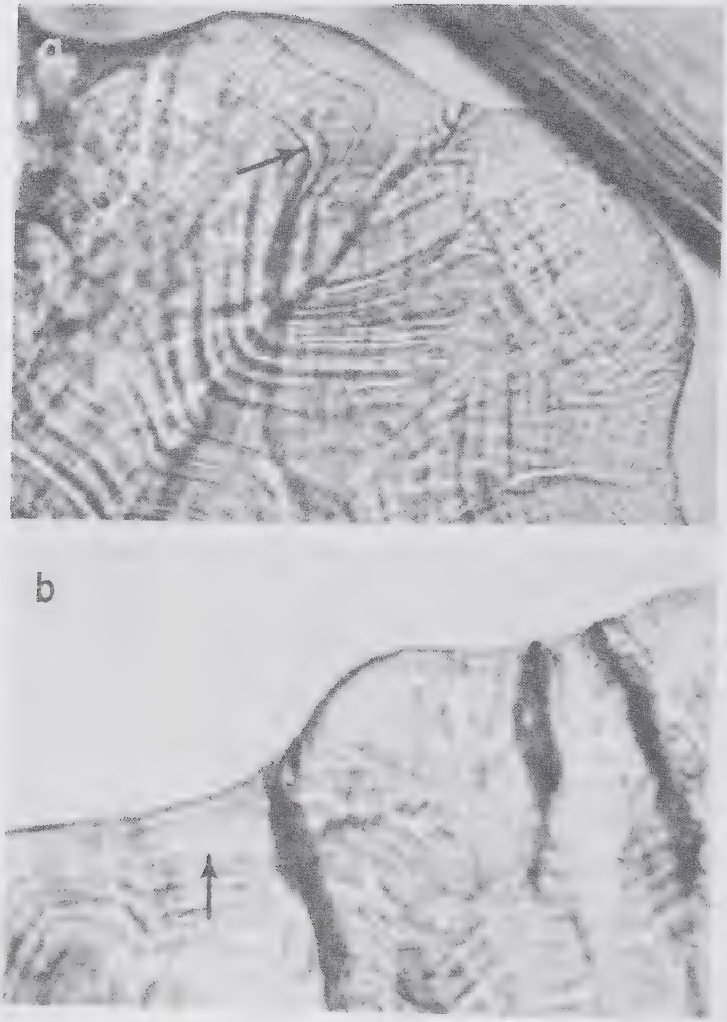

FIGURE 1.—Check mark, indicated by arrow, separates the environmentally marked increments from previous growth increments at a) tip of skipjack tuna sagitta rostrum; b) postrostrum of same skipjack tuna sagitta.

to the feeding period formed primarily on the tips of the rostrum and postrostrum (Figure 1a, b).

The highest count attainable corresponded with the number of days the tuna were fed to satiation, thus confirming the growth increment-day relation (Table 1). The number of increments formed after the check mark usually exceeded the number of feeding days because the tunas continued to live beyond the feeding period. During this latter period, the tunas either received a daily ration or starved. Great care was taken to avoid double counting of an increment where the sagitta was thin. The observations on these specimens were not long term and conditions were not fully controlled. Therefore, these data are considered tentative and in need of replication by rigorous experimental methods.

Wild and Foreman (1980) were able to show a 1:1 (day-to-growth increment) relationship for yellowfin tuna, 40-110 cm FL. However, their day-to-growth increment relation for skipjack tuna was significantly <1:1. Although an experiment where the fish lived in its natural environment was highly desirable, there was no control over variables and a record of variables which the fish might have encountered was unavailable.

Variables such as the amount of food a fish consumes (Struhsaker and Uchiyama 1976; Methot

TABLE 1.—Experimental data on marked daily growth increments in skipjack and yellowfin tunas.

Experimental animals	Fork length (cm)	Feeding period	Date of death per sampling	Length of feeding period (d)	No. of marked increments
Skipjack tuna 3	48.3	23 Aug.-22 Sept.	6 Oct.	30	33
Skipjack tuna 4	45.3	9-14 Oct.	27 Oct.	5	7
Skipjack tuna 5	49.3	15-22 Oct.	27 Oct.	7	8
Skipjack tuna 6	45.0	19-30 Oct.	4 Nov.	11	14
Yellowfin tuna 1	52.2	2-26 Aug.	4 Sept.	24	24
Yellowfin tuna 2	52.0	20 Aug.-19 Sept.	29 Sept.	30	31

and Kramer 1979), temperature (Taubert and Coble 1977; Methot and Kramer 1979), and age of fish (Pannella 1971; Brothers et al. 1976) have been demonstrated to affect the formation of daily growth rings on the sagitta. In our experiments with nehu, skipjack tuna, and yellowfin tuna, the amount of daily ration appeared to have an influence on otolith growth increments. Fishes fed once daily did not have clear otoliths with countable growth increments. Only when the fishes were fed to satiation throughout the day were countable growth increments formed. In the experiment on the effect of winter conditions on the formation of growth increments by Taubert and Coble (1977), the green sunfish, *Lepomis cyanellus*, lowered their activity level and fed less when the temperature fell below 10° C. Wild and Foreman (1980) also suggested that the difference in their results between yellowfin and skipjack tunas may have been due to feeding, citing the differences in the occurrence of full stomachs in the yellowfin and skipjack tunas from the Revillagigedo Islands area examined by Alverson (1963). Thus, it is evident that there is need for further research on the variables affecting day-to-growth increment relation of tuna otoliths.

RESULTS AND DISCUSSION

Skipjack Tuna

A plot of fork length versus age for 51 central Pacific tuna indicated three linear stanzas of growth (Figure 2). A least squares procedure was used to compute the lines of best fit for each stanza (Figure 2, Table 2). Von Bertalanffy growth parameters were also calculated (Figure 2). As there are no means available to statistically compare the von Bertalanffy growth curve, which has three parameters, with the three linear growth stanzas, which have a total of six parameters, the comparison was performed by examining the distribution of residuals (Figure 3). The residuals for the linear growth stanzas were distributed randomly about the x-axis, signifying a good fit (run's test: $Z = 0.39678$, $P \approx 0.6892$). On the other hand, the residuals for the von Bertalanffy curve oscillated about zero and were largest at breakpoints between linear stanzas and at the midpoint of the stanzas, thus suggesting a deviation from randomness (run's test: $Z = -3.32287$, $P<0.001$). Therefore, the linear stanzas appeared to be the preferable growth curve.

TABLE 2.—Length-age regression parameters for the three linear growth stanzas of skipjack tuna: N = number of data and RSS = residual sum of squares.

					Intersections	
Stanzas	N	Intercept	Slope	RSS	Years	Fork length (cm)
1	11	0.0552	58.4167	3.0910		
					0.4616	27.0192
2	35	13.6402	28.9853	17.6038		
					1.9921	71.3812
3	5	51.6918	9.8838	0.2761		
Total RSS				20.9709		

It was noted earlier that the series of three linear growth lines appeared to provide a better fit to our data than the von Bertalanffy growth curve. However, since many of the earlier growth studies use the von Bertalanffy growth curve, it is of interest to compare the von Bertalanffy growth curve of this study with those of other growth studies on the central Pacific skipjack tuna stock (Figure 4). Growth rate estimates by Rothschild (1967) using corrected data of 35 long-term tag returns, by Joseph and Calkins (1969) using Rothschild's uncorrected data, and by Skillman[9] using 356 tag returns obtained during a 2-yr period, were all less than the rate obtained in this study. Brock (1954) analyzed the modal progression in length-frequency distributions obtained over a 5-yr period, and derived a growth curve similar to ours. Both curves show similar growth

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[9] Skillman, R.A. Estimates of von Bertalanffy growth parameters for skipjack tuna, *Katsuwonus pelamis*, from capture-recapture experiments in the Hawaiian Islands. Manuscr. in prep. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, Hawaii.

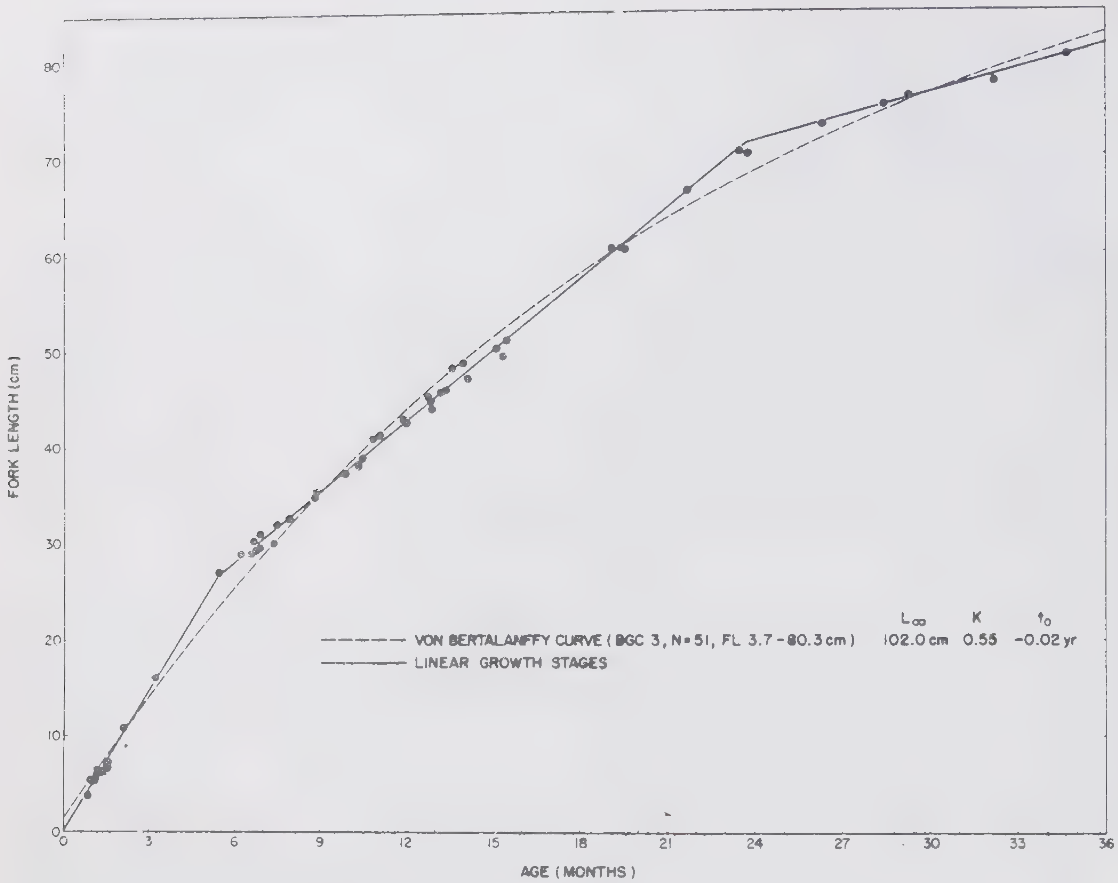

FIGURE 2.—Growth curve of skipjack tuna in the central Pacific as determined by otolith examination. Linear growth stanzas determined by LINFIT (see text). For parameters of growth stanzas, see Table 2.

rates up to 65 cm FL; beyond 65 cm FL, Brock's curve departs from ours and approaches an asymptote more rapidly. The difference in the growth rates above 65 cm may be due to two factors which would affect the modes of large (>6.8 kg) skipjack tuna: differential fishing or total mortality and temperature requirements of skipjack tuna. Barkley et al. (1978) hypothesized that large (>6.8 kg) skipjack tuna required cooler water than small skipjack tuna and therefore could tolerate the warmer surface water for relatively short periods. If so, the catchability of large skipjack tuna would be altered in the surface fishery and length-frequency modes of large skipjack tuna would be underestimated. Our otolith age determinations are not affected by these factors.

Otolith readings were also used to examine the age-length relationship of eastern Pacific skipjack tuna (Figure 5). Of the 20 specimens examined, 11 were caught off Baja California, Mexico. The other nine were caught in the eastern Pacific west of the Inter-American Tropical Tuna Commission's Yellowfin Regulatory Area. Most of these nine specimens had age-length relationships similar to those of fish caught off Baja California, but several had relationships similar to specimens taken in the central Pacific. Indications are that skipjack tuna in the eastern Pacific Ocean off Baja California grew at a slower rate than those in the central Pacific.

Our eastern Pacific skipjack tuna growth curve was compared with those of earlier studies from the eastern Pacific (Figure 5). A growth curve based on the progression of modes in length frequencies (Joseph and Calkins 1969) is similar to our curve; both show good agreement between 40

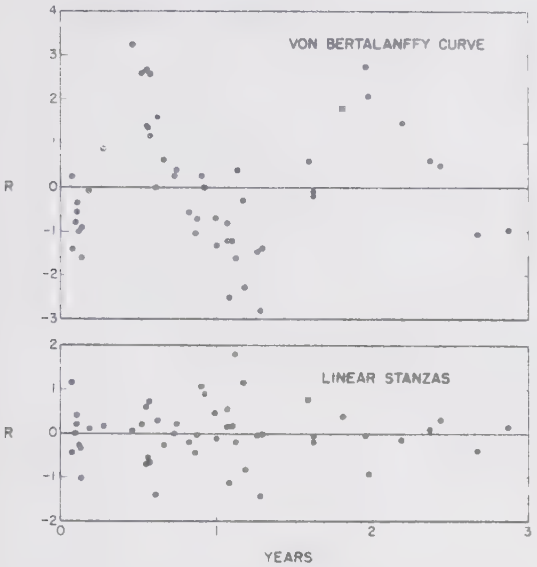

FIGURE 3.—Plot of residuals from von Bertalanffy growth curve and linear growth stanzas of central Pacific skipjack tuna shown in Figure 2.

and 65 cm FL. Growth curves determined from tagging data (Schaefer 1961; Joseph and Calkins 1969) showed slower growth.

The sagittae of five skipjack tuna from Papua New Guinea waters were examined (Figure 6). These fish grew more slowly than those from the central Pacific area.

Central Pacific Yellowfin Tuna

Two distinct stanzas of growth are evident for the sample of 14 central Pacific yellowfin tuna (Figure 7). Linear growth is apparent for about the first 14 mo of life, after which time the data suggest either the beginning of another linear growth phase or an asymptotic growth process. A segmented model with two linear phases was fitted to the data (Table 3). A von Bertalanffy growth equation was also fitted to the data and the following growth parameters were obtained: $L_\infty = 170.3$ cm; $K = 0.3864$, and $t_0 = 0.0366$ yr. Plots of residuals on age for both the segmental model and the von Bertalanffy growth curve were

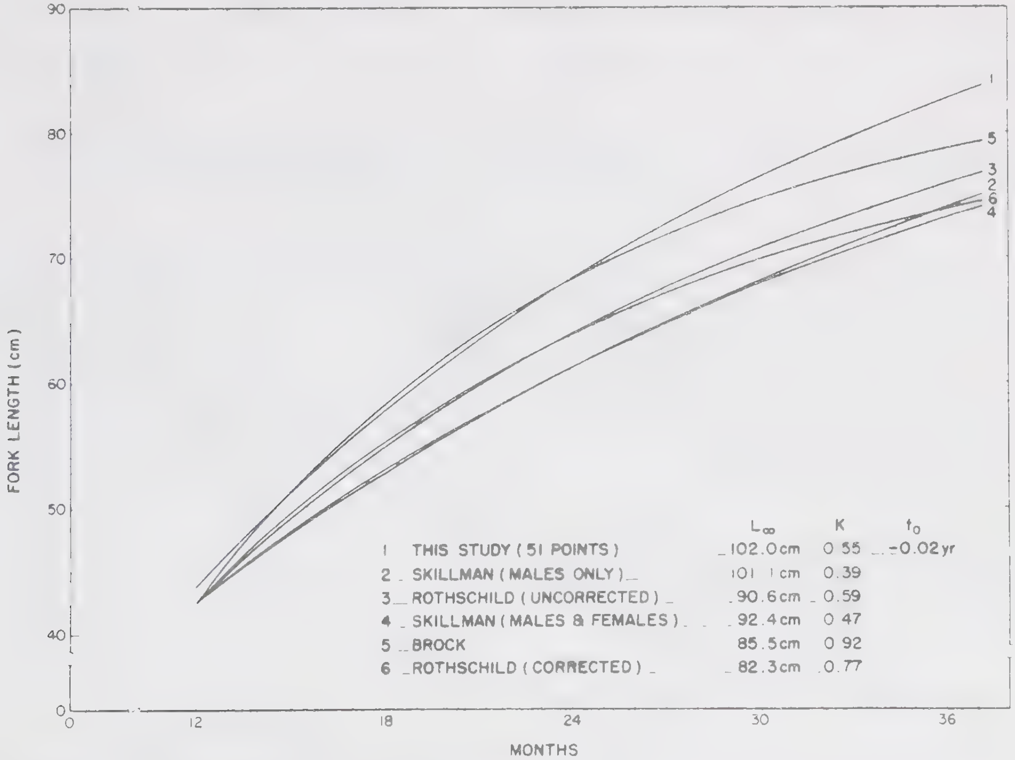

FIGURE 4.—A comparison of von Bertalanffy growth curves determined for central Pacific skipjack tuna (for full references, see text).

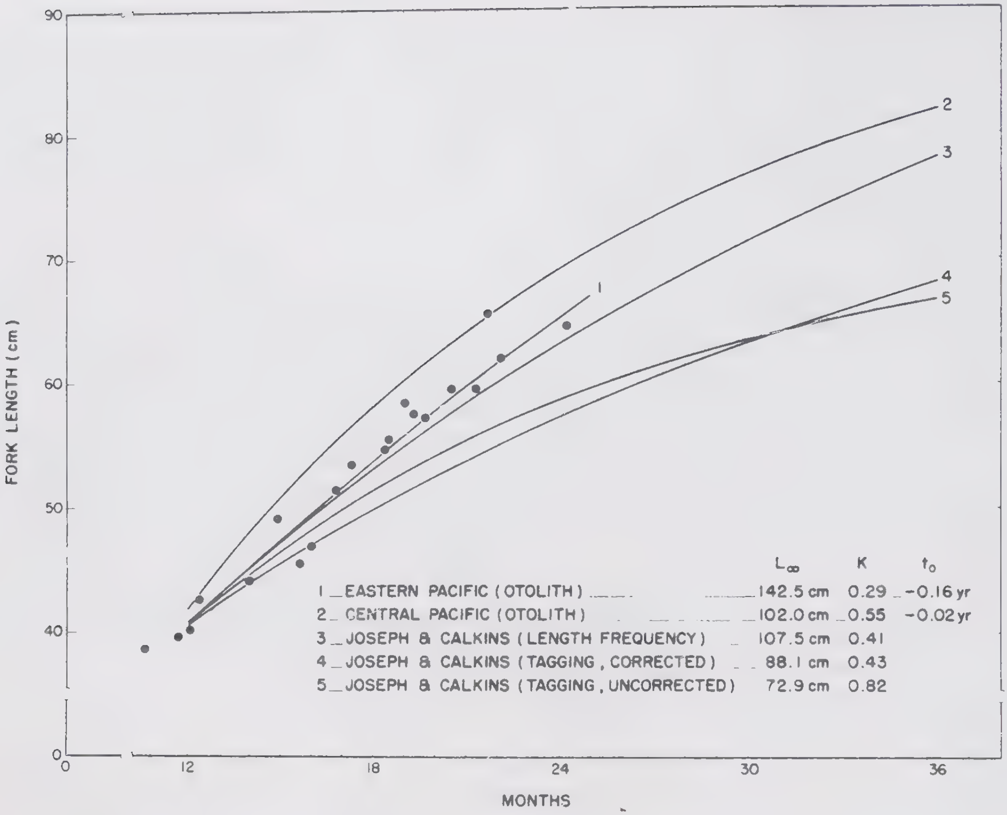

FIGURE 5.—The von Bertalanffy growth curve of skipjack tuna in the eastern Pacific as determined by otolith examination and its comparison with von Bertalanffy growth curves of previous studies from that area and the central Pacific (for full reference, see text).

TABLE 3.—Length-age regression parameters for the two linear growth stanzas of central Pacific yellowfin tuna: N = number of data and RSS = residual sum of squares.

					Intersections	
Stanzas	N	Intercept	Slope	RSS	Years	Fork length (cm)
1	10	0.8831	52.5837	5.7430	1.2047	64.2304
2	4	25.5653	32.0954	0.4620		
Total RSS				6.2050		

compared (Figure 8). As with skipjack tuna, the von Bertalanffy model gives a poorer fit than the linear segmental model. Although the probability for the distribution of residuals to be randomly distributed along the von Bertalanffy curve was significant at $P = 0.05$ (run's test, table of critical values: $r = 7$, $n_1 = 7$, $n_2 = 7$), clustering of pluses and minuses occurred. The run's test for the linear segmental model also showed randomness ($r = 9$, $n_1 = 6, n_2 = 8$; table of critical values, $P < 0.05$), and was an improvement over the von Bertalanffy curve with the increase in the number of runs from 7 to 9.

The results of our study on yellowfin tuna within the size range examined agree with most earlier studies for this species from the eastern and central Pacific Ocean. The results of aging by scales (Yabuta et al. 1960) and modal progression in length-frequency distributions (Hennemuth 1961) are given for comparison (Figure 6). It has been suggested that growth of yellowfin tuna in the eastern Pacific between the lengths of 50 and 100 cm is linear and that growth rates are 0.6-1.0 mm/d (Inter-American Tropical Tuna Commission 1972, 1974).

CONCLUSIONS

Daily growth information provides much greater insight into the growth patterns of teleost

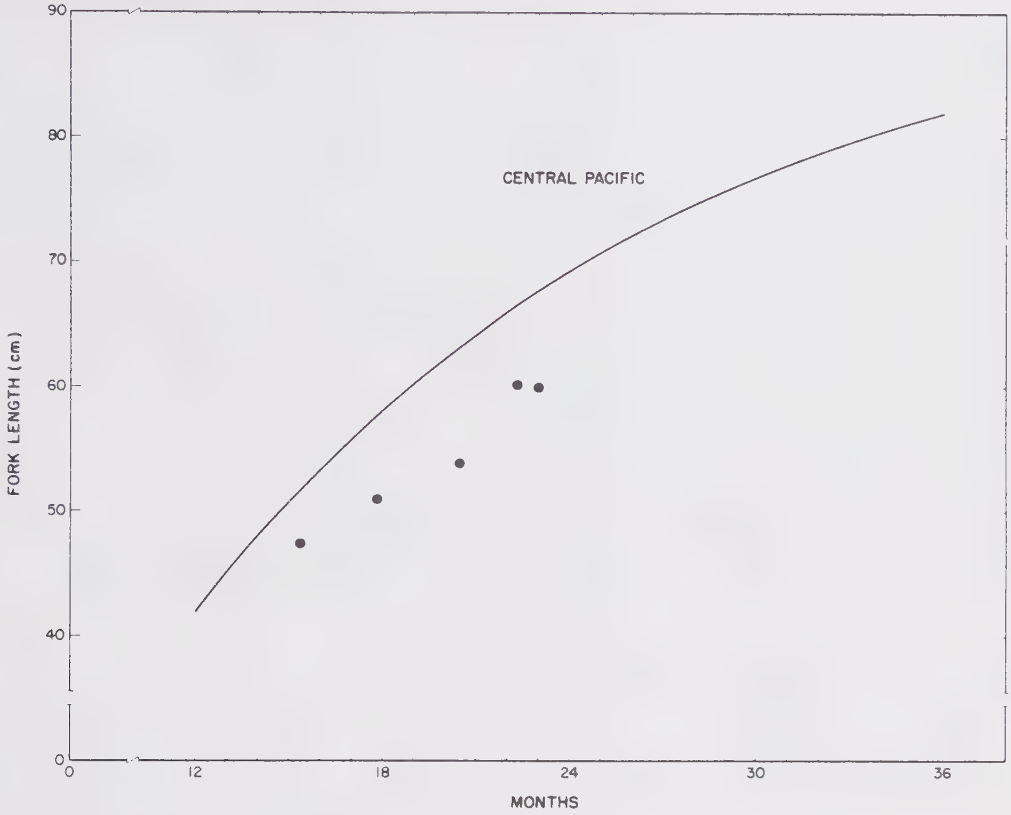

FIGURE 6.—Age determinations (points) of skipjack tuna from Papua New Guinea and comparison with the von Bertalanffy growth curve of central Pacific skipjack tuna derived in this paper.

fishes than can be gleaned using traditional annual techniques. Data presented here suggest three stanzas of linear growth for central Pacific skipjack tuna ranging in size from 3 to 80 cm FL, and that central Pacific yellowfin tuna from 7 to 93 cm FL have at least one stanza of linear growth.

Our assumption that the growth increments on the sagittae of skipjack and yellowfin tunas are deposited daily was supported by the deposition of experimentally induced increments on the sagittae of captive fishes and the relatively good agreement of our skipjack tuna and yellowfin tuna growth curves with those of previous studies utilizing other growth estimating techniques such as progression of modes in length-frequency distributions and interpretation of other hard parts. Growth studies on tunas based on tagging experiments have usually slower growth rates.

Otolith readings on specimens from three different areas suggest that there are geographical variations.

Estimation of growth rates from daily growth increments on sagittae is subject to at least two possible sources of error. One is that increments may not be deposited due to variables such as an inadequate ration, diet, temperature, age of fish, or during some physiologically stressful activity, such as reproduction. This is apparently the case for three species of boreal gadoids investigated by Pannella (1971). Another source is differential error during increment counting. If fewer rings are counted than actually exist, this, in addition to nondeposition of daily increments, would result in overestimation of growth rate.

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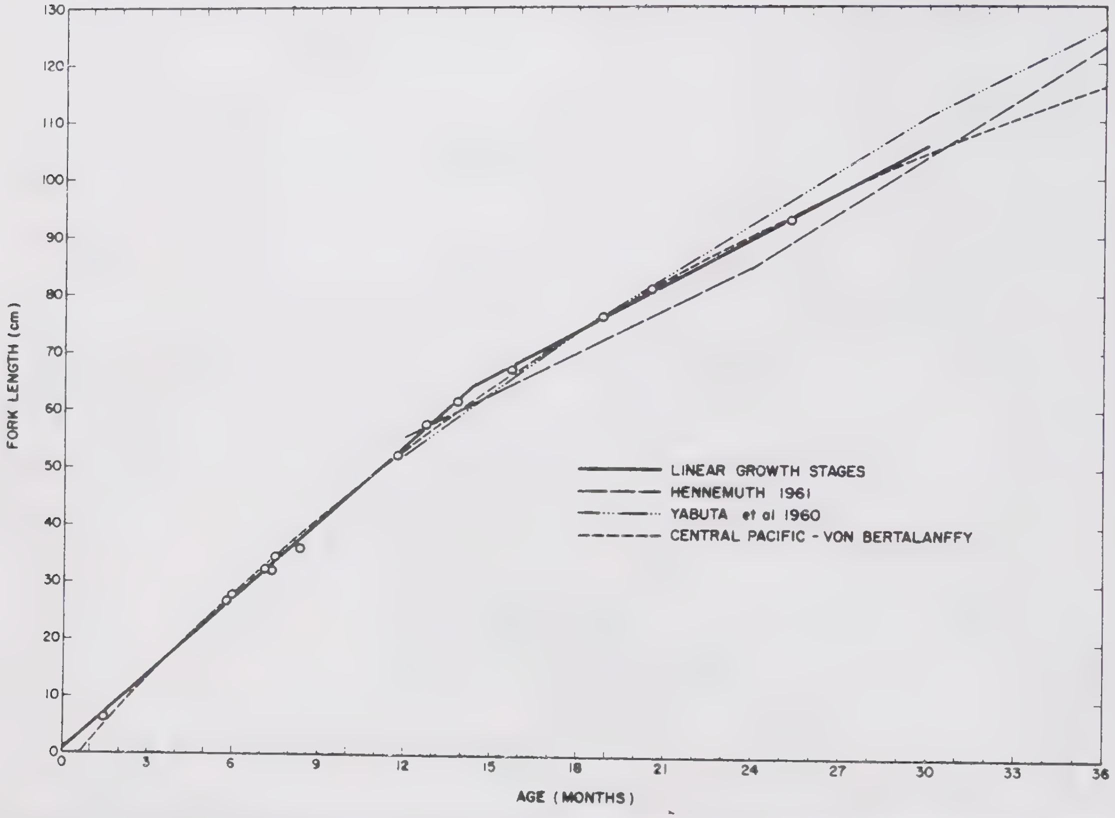

FIGURE 7.—Growth curve of yellowfin tuna in the central Pacific as determined by otolith examination and compared with growth curves of previous studies from that area and the eastern Pacific. Linear growth stanzas determined by LINFIT (see text). For parameters of growth stanzas, see Table 3.

pen and Howard O. Yoshida for their editorial help. We are especially indebted to Gary L. Kamer and Jeffrey J. Polovina for assisting with the statistical problems encountered. Marian Y. Y. Yong assisted with the data processing and Glen H. Sugiyama verified some of the age determinations. We are grateful to Sherry Steffel for sharing her data on feeding records and otoliths of skipjack and yellowfin tunas from her experiment.

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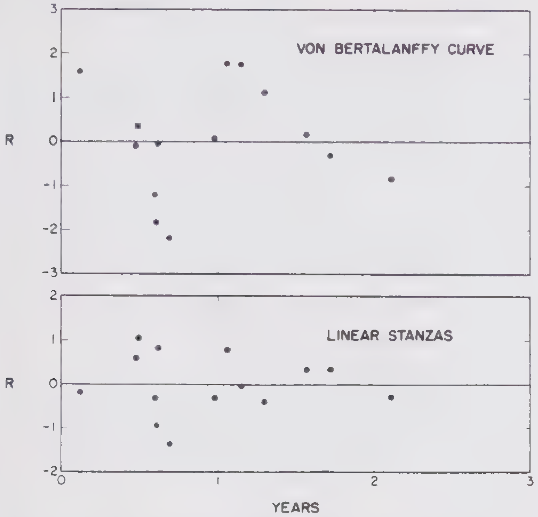

FIGURE 8.—Plots of residuals from von Bertalanffy growth curve and linear stanzas of central Pacific yellowfin tuna shown in Figure 7.

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ELECTROPHORETIC, MORPHOMETRIC, AND MERISTIC STUDIES OF SUBPOPULATIONS OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*[1]

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We investigated the population structure of northern anchovy found between southern Baja California and Newport, Oregon. We used electrophoretic, morphometric, and meristic methods in our studies, and the results indicate the presence of three distinct anchovy subpopulations.

INTRODUCTION

Hubbs (1925) and McHugh(1951) found subpopulations of the northern anchovy along the west coast of the United States and Mexico. For more effective management of the growing United States and Mexican anchovy fisheries, knowledge of the number of subpopulations and how they are distributed geographically is necessary, as is a feasible method of readily distinguishing the subpopulations. In this study we used electrophoretic methods to distinguish subpopulations and delineate their geographical range; morphometric and meristic comparisons were made between these subpopulations.

Transferrin Electrophoresis

Transferrin is the vertebrate blood serum protein responsible for binding iron. Transferrin polymorphism has been reported in a variety of teleost fishes by several authors including Creyssel et al. (1964), Moller (1966), Moller and Naevdal (1966), Barrett and Tsuyuki (1967), Fujino and Kang (1968), and Utter (1969).

Morphometrics

Hubbs (1925) found small morphometric differences in samples of *Engraulis mordax* collected from San Francisco to southern California. He also described a distinct subspecies, *Engraulis mordax nanus,* which he found inhabiting the brackish waters of San Francisco Bay. We were unable to collect the bay anchovy.

Meristics

McHugh (1951) found three subpopulations of northern anchovy: one off British Columbia to northern California, one off southern California and northern Baja California, and one off central and southern Baja California. He based his conclusion on the mean values he found in five different meristic characters. Hubbs (1925) found a distinct difference in vertebral numbers when he com-

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pared open ocean anchovies with bay anchovies from San Francisco Bay. He also found small differences in vertebral numbers between samples of open ocean anchovies from San Francisco to southern California.

MATERIALS AND METHODS

Transferrin Electrophoresis

Anchovies were collected from Newport, Oregon, to the southern end of Baja California (Table 1). Availability of samples was limited since the anchovies had to be kept alive until the blood samples were taken; dead or preserved fish could not be used. The samples came primarily from commercial live bait vendors and from short-duration surface hauls made with a midwater trawl. We tried to obtain 50 to 100 fish per sample, but this was frequently impossible. In a few cases, two smaller samples taken very closely together in time and space were combined into one; other samples which contained less than 35 readable transferrin types and could not be combined were not used in the population analysis.

TABLE 1. Sampling Data for Northern Anchovy Subpopulation Genetic Testing and Percent Occurence of Transferrin Alleles in the Samples

Site	*Location*	*Date*	*Number of fish*	*Percent transferrin alleles* Tf^A	Tf^B	Tf^C	Tf^D
		Northern subpopulation					
1	Newport, Oregon	July 1969	84	81.6	8.3	5.4	4.8
2	Newport, Oregon	July 1970*	66	78.0	13.6	5.3	3.0
3	Eureka, California	July 1970	38	77.6	14.5	5.3	2.6
4	Salt Point, California	July 1970	54	80.6	13.0	3.7	3.4
5	Monterey, California	November 1969	106	76.9	12.3	5.7	5.2
		Central subpopulation					
6	San Francisco, California	April 1968	48	85.4	7.3	7.3	0
7	San Francisco, California	May 1968	64	72.7	16.4	10.9	0
8	Monterey, California	May 1968	87	76.4	13.8	9.8	0
9	Monterey, California	October 1967	54	82.4	7.4	10.2	0
10	Newport, California	August 1968	94	80.8	10.1	8.0	1.1
11	San Diego, California	July 1968	47	81.9	9.6	7.4	1.1
12	San Diego, California	July 1968	100	80.5	12.0	7.5	0
13	Ensenada, Mexico	May 1968	37	82.4	9.5	8.1	0
14	Ensenada, Mexico	July 1968	94	80.8	11.2	8.0	0
15	Todos Santos Is, Mexico	August 1969	48	83.3	11.5	5.2	0
16	30° 50.5′N	August 1969	43	82.6	11.6	4.7	1.2
17	30° 17′N	January 1969	67	84.3	11.9	3.7	0
18	30° 12′N	January 1969	70	84.3	10.0	5.7	0
19	30° 09′N	March 1968	43	84.9	7.0	7.0	1.2
20	29° 33′N	November 1967	36	80.6	11.1	8.3	0
		Southern subpopulation					
21	28° 33.2′N	November 1967	83	91.1	4.8	4.2	0
22	27° 55.5′N	November 1967	64	90.6	5.5	3.9	0
23	27° 52.5′N	November 1967	87	87.9	6.3	5.8	0
24	27° 06.0′N	November 1967	75	88.7	6.7	4.7	0
25	27° 04.0′N	November 1967	72	87.5	6.9	5.6	0
26	24° 30.0′N	November 1967	72	88.2	6.2	5.6	0

We collected blood samples from live fish by inserting a heparinized capillary tube through the gill opening into the dorsal aorta. The tube was allowed to flow full of blood and then was sealed on the bottom with a bit of clay. Filled capillary tubes were then centrifuged at about 2000 *g* for 5 min. When samples were not electrophoresed immediately, they were frozen with dry ice and stored at 0° C.

When a sample was ready to be electrophoresed, the thawed capillary tube was broken off at the interface of the serum and red cells; the cells were discarded. A piece of absorbent paper was touched to the end of the capillary tube to absorb the serum until a colum of liquid 33 mm long remained; this was equivalent to 25 µl. The 25 µl of serum were mixed with 10 µl of radioactive Fe^{59} and allowed to incubate for at least 10 min. A slot cut in the starch gel was filled with the mixture and electrophoresed for 1 h 40 min at 150 v in a horizontal, thin layer, starch gel apparatus. After electrophoresis was complete, we prepared autoradiographs of the gels using a modification of the method of Giblett, Hickman, and Smithies (1959).

We examined the hypothesis that each band represented a specific transferrin, controlled by a different autosomal allele at a single locus. First, we verified that "artificial heterozygotes" produced by mixing equal parts of sera from the appropriate homozygous types produced electrophoretic patterns indistinguishable from the natural heterozygous types. Secondly, we examined the statistical distributions of phenotypes in populations thought to be in equilibrium with respect to the alleles found.

The frequency of occurrence of the transferrin alleles in anchovy samples was calculated as $1/N\ (0_{ii}+\frac{1}{2}\Sigma 0_{ij})$, where i = A, B, C, D (representing alleles) and $j \neq i$. For examle, O_{AA} is the number of phenotypes AA observed and N is the total number of fish in the sample. Allocation of samples to the subpopulations was determined by cluster analysis (Sneath and Sokal 1973) of the percentage distributions of alleles for each sampling site. The clustering sequence was obtained by identifying the two sites most alike, combine the two and clustering with the next most similar site, etc. The computer program used was BMDP2M written at the Health Sciences Computer Facility, University of California, Los Angeles. Clustering was by Euclidean distance (the square root of the sums of squares of differences between percent alleles).

Morphometrics

Morphometric measurements were made with a vernier caliper on formalin preserved anchovies which had been classified to subpopulation by transferrin gene frequencies. Head length, eye diameter, snout to post-orbital margin, head depth, and body depth were measured. Allometric regressions ($\ln y = a + b \ln x$) were calculated for each of the five morphometric measurements, where x is the standard length (SL).

Meristics

We took all meristic counts from formalin preserved samples which we had classified as northern, central, or southern subpopulation anchovies on the basis of transferrin gene frequencies. Counts were made from x-ray plates with the aid of a binocular dissecting microscope. Vertebrae, anal fin rays, and dorsal fin rays were counted. The vertebral counts did not include the basioccipital nor the hypural.

RESULTS AND DISCUSSION

Transferrin Electrophoresis

We found that transferrin polymorphism in the northern anchovy orginates in a genetic system of four co-dominant autosomal alleles, each controlling the formation of a single protein with a specific anodal migration rate when electrophoresed in starch gel. The four iron-binding protein bands were designated A, B, C, and D. The migration distance in a standard run was 23.4 mm for band A, 21.1 mm for band B, 19.0 mm for band C, and 16.2 mm for band D (Figure 1).

Northern (sites 1–5) and southern (sites 21–16) groups were clearly distinguished by cluster analysis (Figure 2) of the transferrin alleles' percentage of occurrence (Table 1). A central group (site 6 and sites 9–20) was also evident. However, samples taken at sites 7 (San Francisco) and 8 (Monterey) during May of 1968 were distinct from all groups. These samples were anomalous in that they were not intermediate between the major groupings but rather represented extreme levels for all alleles; thus a mixture of populations or interbreeding does not suffice as a rational explanation. These anomalies are believed to be due to occasional indistinct separation of the first three bands within the gel. The absence of the D allele separates these samples from the northern group and the relative frequencies of the B and C alleles separates them from the southern group; thus we included them within the central subpopulation. There is an overlap in the geographical range of samples attributed to the northern and central subpopulations; the southernmost sample from the northern subpopulation was taken in Monterey in November 1969, and the northernmost samples from the central subpopulation were taken from San Francisco Bay in April and May 1968, an overlap of about 70 nautical miles. This does not mean that the two subpopulations were necessarily present in these areas at the same time; instead, both subpopulations may tend to move north in the spring and summer and return toward the south in the fall and winter. Anchovy tagging studies conducted by California Department of Fish and Game support the north and south movements (Haugen, Messersmith, and Wickwire 1969).

The northern subpopulation was distinguished from the other two by the Tf^D allele which was not found in the southern subpopulation, was rare in the central subpopulation (0.2%), but occurred at a rate of 4.02% in the northern subpopulation (Table 2). The central subpopulation was distinguished from the southern one by the frequency of occurrence of Tf^A and Tf^B alleles. Tf^A occurred at a rate of 88.96% in the southern subpopulation compared to 81.17% in the central one; Tf^B occurred at 11.0% in the central subpopulation and only 6.07% in the southern one. Chi-square goodness of fit tests on observed numbers of phenotypes for the three subpopulations versus the expected numbers calculated from the Hardy-Weinberg equilibrium formula (Table 2) support the four-allele hypothesis.

Similarity or dissimilarity of the subpopulations was judged on the basis of the observed phenotypic distributions with northern-central and central-southern differences treated separately. We found the rare allele to be important in discriminating the northern subpopulation, whereas the predominant alleles provided the discriminatory power for the central and southern subpopulations (Table 3). To avoid difficulties with expectations in the statistical tests, all combinations of the Tf^D allele were grouped for the chi-square tests. The results of the chi-square tests for independence $[\Sigma(O-E)^2/E]$ are as follows:

North-central $X^2 = 61.99$, d.f. = 6; $P < .005$
Central-southern $X^2 = 27.88$; d.f. = 6; $P < .005$

Both indicate highly significant differences between subpopulations.

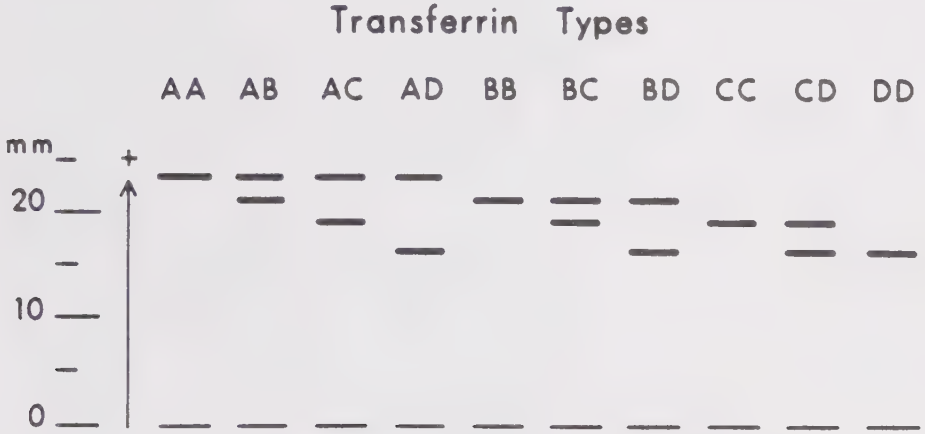

FIGURE 1. Transferrin pattern types found in northern anchovy.

TABLE 2. Gene Frequencies in the Three Northern Anchovy Subpopulations and the Observed and Expected Number of Phenotypes. The Expected Numbers were Calculated from the Hardy-Weinberg Equilibrium Formula

Allele	*Northern (N)*		*Central (C)*		*Southern (S)*	
Tf^A	78.88%		81.17%		88.96%	
Tf^B	11.92		11.00		6.07	
TF^C	5.17		7.56		4.97	
Tf^D	4.02		0.27		0.00	
Phenotype	*Expected*	*Observed*	*Expected*	*Observed*	*Expected*	*Observed*
AA	216.52	215	614.05	619	358.51	360
AB	65.47	67	166.40	161	48.93	47
AC	28.39	30	114.44	111	40.03	39
AD	22.09	22	4.05	3	0.00	0
BB	4.95	4	11.27	13	1.67	2
BC	4.29	4	15.50	17	2.73	4
BD	3.34	4	0.55	1	0.00	0
CC	0.93	0	5.33	6	1.12	1
CD	1.45	2	0.38	1	0.00	0
DD	0.56	0	0.01	0	0.00	0

$X_N^2 = 0.36$; d.f. = 5; $P > 0.995$
$X_C^2 = 1.38$; d.f. = 4; $P > 0.750$
$X_S^2 = 0.78$; d.f. = 3; $P > 0.750$

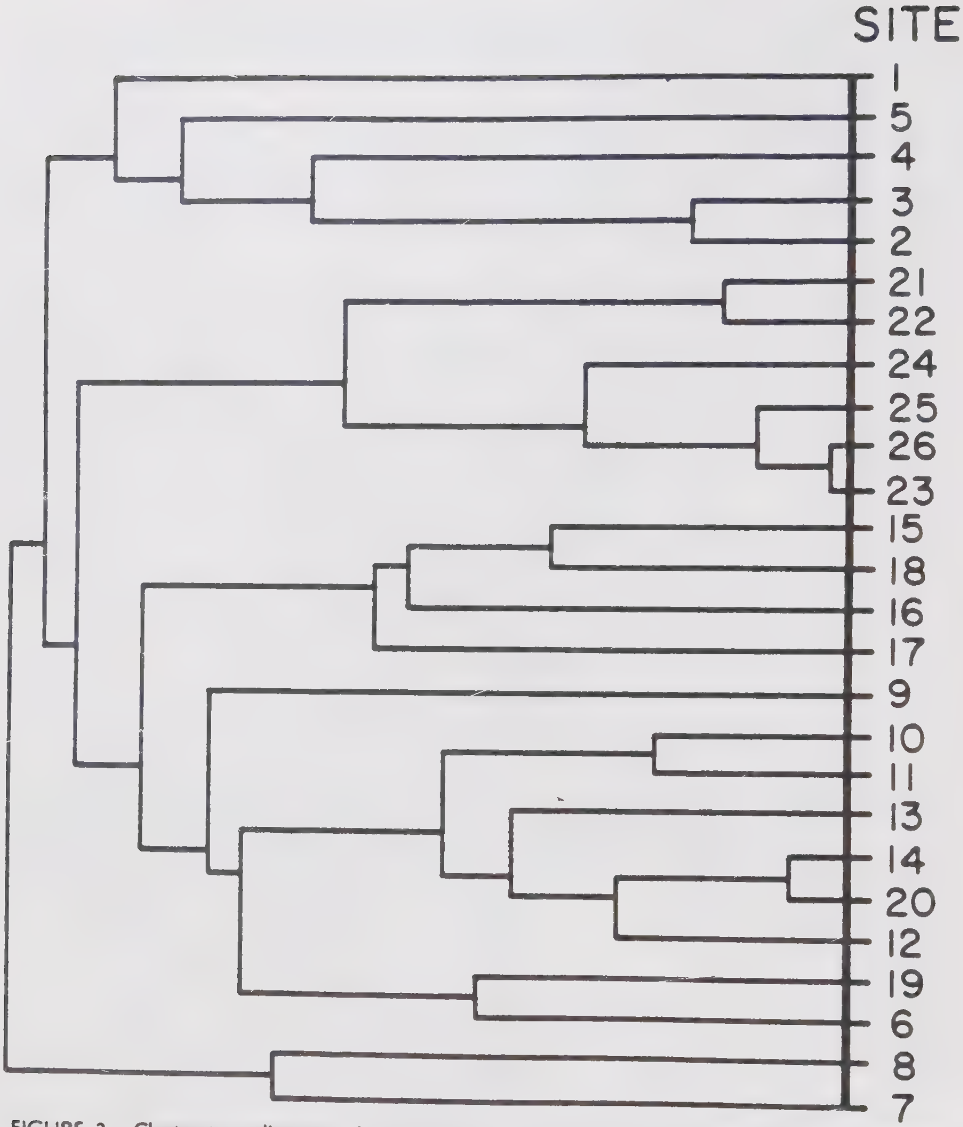

FIGURE 2. Cluster tree diagram of sample sites by proportion of transferrin alleles. Clustering sequence is determined by the distance of the vertical bars from the solid vertical line. Example: 23 and 26 are most similar, then 14 and 20, etc. Subpopulations identified are northern (1–5), southern (21–26) and central (6–20).

Thus, the transferrin data support the conclusion of McHugh (1951) that there are three subpopulations of northern anchovies in the area. The close agreement in numbers of transferrin types observed with the expected numbers (Table 2) calculated from the Hardy-Weinberg equilibrium formula indicates three genetically distinct subpopulations with little or no interbreeding; a northern one from about Monterey north, a central one from San Francisco to about 29° N lat, and a southern one south of 29° N (Figure 3).

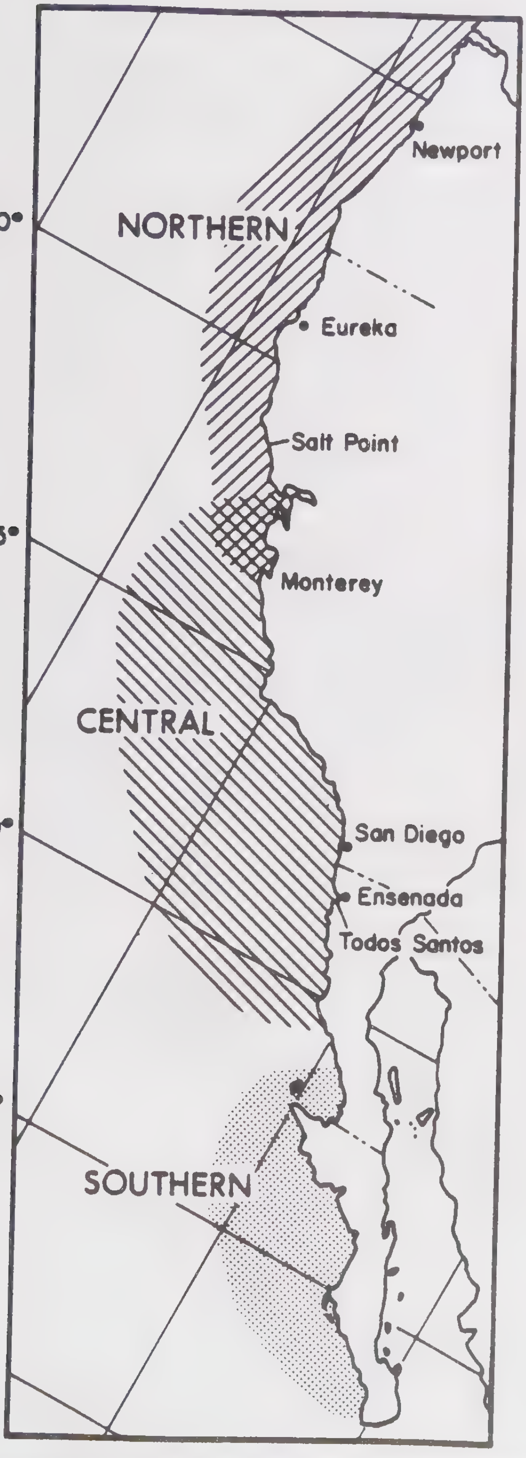

FIGURE 3. Distribution of three northern anchovy subpopulations based on transferrin allele frequencies.

TABLE 3. Observed and Expected Numbers of Phenotypes Assuming No Differences Between Subpopulations

		Phenotype							
		AA	*AB*	*AC*	*BB*	*BC*	*CC*	*AD+BD+ CD+DD*	*Total*
Northern	O	215	67	30	4	4	0	28	348
	E	226.7	62.0	38.3	4.6	5.7	1.6	9.0	
Central	O	619	161	111	13	17	6	5	932
	E	607.2	166.0	102.7	12.4	15.3	4.4	24.0	
TOTAL		834	228	141	17	21	6	33	1280

		AA	*AB*	*AC*	*BB*	*BC*	*CC*	*AD+BD+ CD+DD*	*Total*
Central	O	619	161	111	13	17	6	5	932
	E	658.8	140	100.9	10.1	14.1	4.73	3.4	
Southern	O	360	47	39	2	4	1	0	453
	E	320.2	68	49.1	4.9	6.9	2.3	1.6	
TOTAL		979	208	150	15	21	7	5	1385

Morphometrics

Morphometric measurements were taken on 613 fish (Table 4). Except for eye diameter, there was no evidence that the slope coefficients b differed among the subpopulations (Table 5) test for parallel lines. The slope for eye diameter in the northern group differed from those of the southern and central, but the latter two showed no statistical difference. Only body depth indicated direct proportionality, i.e., b was not significantly different from unity.

TABLE 4. Sampling Data for Northern Anchovy Morphometric and Meristic Testing

Subpopulation	*N*	*Mean standard length (mm)*	*Range*	*Standard deviation*
Northern	206	97.20	77–135	10.01
Central	225	104.47	70–136	15.39
Southern	182	90.11	50–116	13.65

Because the slope coefficients for eye diameter differed among subpopulations, no test for a common regression line was performed for eye diameter. All other tests for a common regression line, i.e., the same slope and intercept, were highly significant ($P < 0.01$). In each instance, the more similar of the two subpopulations were also tested for a common relationship. Body depth indicated no difference between the southern and central subpopulations. Otherwise all differences between subpopulations were significant at $P < 0.05$. The analysis of covariance is not entirely appropriate for morphometric data since both variates are subject to error, especially for field sampling where the size range of the samples is rarely the same and cannot be controlled. It is well to insist on a conservative level of statistical significance; therefore, we calculated the estimated morphometric measurements for a 70-, 100-, and 130-mm anchovy from each subpopulation (Table 6). Southern subpopulation anchovies showed a distinctly longer head, larger eye, and longer snout to post-orbit than did either central or northern ones. Northern subpopulation anchovies exhibited a deeper body, and northern and southern subpopulation anchovies showed a slightly deeper head than did those of the central stock. Average morphometric measurements calculated for 10-mm intervals from 70 to 120 mm show the consistent pattern of differences between the subpopulations at all sizes (Table 7).

TABLE 5. Covariance Analysis for the Three Northern Anchovy Subpopulations: SL = Standard Length

Subpopulation		*Test for common regression line*	*Test for parallel lines*
	Head depth (hd)		
Southern	$\ln L_{hd} = -1.637 + .967 \ln L_{SL}$		
Central	$\ln L_{hd} = -1.661 + .968 \ln L_{SL}$	$F_{4,407} = 12.79^*$	$F_{2,407} = 0.10^{**}$
Northern	$\ln L_{hd} = -1.570 + .955 \ln L_{SL}$		
	Body depth (bd)		
Southern	$\ln L_{bd} = -1.982 + 1.052 \ln L_{SL}$		
Central	$\ln L_{bd} = -1.928 + 1,039 \ln L_{SL}$	$F_{4,407} = 16.00^*$	$F_{2,407} = .54^{**}$
Northern	$\ln L_{bd} = -1.770 + 1.012 \ln L_{SL}$		
	Eye diameter (ed)		
Southern	$\ln L_{ed} = -1,551 + .753 \ln L_{SL}$		
Central	$\ln L_{ed} = -1.366 + .692 \ln L_{SL}$		$F_{2,407} = 8.37^*$
Northern	$\ln L_{ed} = -2.235 + .882 \ln L_{SL}$		
	Snout to post-orbit (po)		
Southern	$\ln L_{po} = -1.273 + .823 \ln L_{SL}$		
Central	$\ln L_{po} = -1.313 + .816 \ln L_{SL}$	$F_{4,407} = 125.04^*$	$F_{2,407} = 2.76^{**}$
Northern	$\ln L_{po} = -1.042 + .755 \ln L_{SL}$		
	Head length (hl)		
Southern	$\ln L_{hl} = -0.850 + .932 \ln L_{SL}$		
Central	$\ln L_{hl} = -1.027 + .955 \ln L_{SL}$	$F_{4,407} = 158.92^*$	$F_{2,407} = 2.56^{**}$
Northern	$\ln L_{hl} = -0.784 + .900 \ln L_{SL}$		

* Significant $P \leq .01$
** Not significant

TABLE 6. Estimated Morphometric Measurements of 70, 100, and 130 mm Standard Length Northern Anchovies Expressed as Percent of Standard Length

Length	*Subpopulation*	*Head length*	*Eye diameter*	*Snout to post-orbit*	*Head depth*	*Body depth*
	Northern	29.8	6.5	12.4	17.2	17.9
70	Central	29.6	6.9	12.3	16.6 *	17.2
	Southern	31.9 *	7.4 *	13.2 *	16.9	17.2
	Northern	28.8	6.2	11.4	16.9	18.0 *
100	Central	29.1	6.2	11.5	16.4 *	17.4
	Southern	31.1 *	6.8 *	12.4 *	16.7	17.5
	Northern	28.1	6.0	10.7	16.7	18.0 *
130	Central	28.8	5.7	11.0	16.2 *	17.6
	Southern	30.6 *	6.4 *	11.8 *	16.6	17.7

* Significant difference ($P \leq 0.01$) between subpopulations within length group.

Hubbs (1925) also reported longer head length (31.9% SL) for a San Francisco Bay subspecies *Engraulis mordax nanus* which also had a greater body depth (19.7% SL) than did the open ocean anchovies (18.1% SL).

Mais (1974) reported that southern subpopulation anchovies are much smaller than central stock anchovies. Of the 2,332 fish he measured from 96 samples collected in more than 5½ yr south of lat 28°30′ N, less than 10% exceeded 106 mm total length (the minimum legal limit of the California anchovy reduction fishery), while 79% of the central stock anchovies were 106 mm or greater. Southern anchovies were significantly smaller than central ones at all ages and nearly attained their maximum length by age 3, while central subpopulation anchovies continued to grow for at least 3 more years.

TABLE 7. Average Morphometric Measurements (mm) in Three Northern Anchovy Subpopulations in 10 mm Intervals of Standard Length; N = Northern; C = Central; S = Southern Subpopulations.

Interval		*Standard length*	*Body depth*	*Head depth*	*Head length*	*Snout-postorbital*	*Eye diameter*	*Number of observations*
	N							0
70– 79	C	75.5	12.8	12.4	22.4	9.2	5.2	24
	S	75.6	13.0	13.0	24.9	10.3	5.9	34
	N	86.2	15.9	15.0	25.2	10.3	5.5	42
80– 89	C	84.0	14.9	14.6	24.9	10.1	5.5	3
	S	83.7	14.4	14.0	26.7	10.9	6.1	36
	N	92.9	16.4	15.5	27.0	10.8	5.8	91
90– 99	C	95.4	16.7	15.8	27.7	11.1	5.9	62
	S	95.0	16.5	15.8	29.4	11.8	6.4	51
100–109	N	105.1	18.9	17.7	30.0	11.8	6.4	33
	C	103.6	18.2	16.8	29.7	11.6	6.3	51
	S	103.5	18.3	17.3	31.7	12.6	6.8	42
110–119	N	112.1	20.5	19.1	31.9	12.5	6.9	37
	C	114.2	20.1	18.9	33.1	12.9	6.8	37
	S	111.6	19.8	18.6	33.9	13.4	7.3	10

Meristics

Vertebrae

Northern subpopulation anchovies had the greatest mean number of vertebral centra (Table 8). The mean for the central subpopulation was significantly less than that of the northern subpopulation ($d = 0.46$; $F_{1,404} = 41.83$; $p < 0.001$). This was also the case for the southern subpopulation with regard to the northern one ($d = 0.43$; $F_{1,384} = 49.44$; $p < 0.001$). There was no significant difference between central and southern subpopulation mean number of vertebrae ($d = 0.03$; $F_{1,380} = 0.16$; $p < 0.25$).

Hubbs (1925) reported a mean number of 44.73 vertebrae for offshore northern anchovies off San Francisco, which is very close to the 44.75 we found for the northern subpopulation. When we partitioned McHugh's (1951, Tables 2 and 3) vertebral data into probable subpopulations (northern, central, or southern) merely on the basis of location of capture, we calculated his northern subpopulation samples to have a mean of 44.74 vertebrae, again in good agreement with ours. His southern subpopulation samples had a mean of 44.32 vertebrae, identical to ours.

TABLE 8. Meristic Analysis of the Three Subpopulations of Northern Anchovies: $\bar{x}$ = Mean, S = Standard Deviation, and S = Standard Error of Mean

	No.	*Range*	$\bar{x}$	S	$S_{\bar{x}}$
Vertebrae					
Northern subpopulation	206	43–46	44.75	0.6325	0.0441
Central subpopulation	200	42–46	44.29	0.7994	0.0565
Southern subpopulation	182	42–45	44.32	0.5734	0.0425
Anal fin rays					
Northern subpopulation					
Male	136	20–24	22.18	0.9043	0.0775
Female	70	20–25	22.20	0.9869	0.1180
TOTAL	206	20–25	22.19	0.9308	0.0649
Central subpopulation					
Male	94	19–25	22.43	1.1499	0.1186
Female	106	19–25	22.36	0.9481	0.0921
TOTAL	200	19–25	22.39	1.0456	0.0739
Southern subpopulation					
Male	109	20–25	22.53	1.0850	0.1039
Female	64	20–25	22.64	1.0445	0.1306
TOTAL	173	20–25	22.58	1.0686	0.0808
Dorsal fin rays					
Northern subpopulation					
Male	136	15–18	16.26	0.5962	0.0511
Female	70	15–17	16.43	0.6272	0.0750
TOTAL	206	15–18	16.32	0.6108	0.0426
Central subpopulation					
Male	94	15–18	16.46	0.6336	0.0654
Female	106	15–18	16.37	0.6666	0.0647
TOTAL	200	15–18	16.41	0.6512	0.0460
Southern subpopulation					
Male	110	15–18	16.35	0.6146	0.0586
Female	65	15–17	16.43	0.6116	0.0759
TOTAL	180 *	15–18	16.37	0.6075	0.0453

* Includes five juveniles.

When we compared the central subpopulations, however, we calculated a mean of 44.88 vertebrae for his samples, which is 0.59 greater than ours. His data indicated a high degree of variability from month to month and year to year. For instance, his data for the mean number of vertebral centra in anchovy post-larvae off southern California (McHugh 1951, Table 4) was 44.21 in 1945, 44.69 in 1947, 44.84 in 1948, and 44.65 in 1949.

Anal Fin Rays

McHugh (1951) reported strong evidence for sexual dimorphism in the number of anal fin rays, with those of males exceeding those of females by 0.13 rays. Our data did not indicate such dimorphism. When all of our samples were combined according to sex, fin rays of females exceeded those of males by only 0.02 rays. When each subpopulation was tested separately for sexual dimorphism, the greatest difference found (Table 8) was in the southern subpopulation where females exceeded males by 0.11 anal fin rays, which was not significant ($F_{1,171} = 0.43$; $p > 0.25$).

When we compared both males and females combined for each of the three subpopulations, we found that the northern subpopulation had a mean anal fin ray count 0.20 less than that of the central subpopulation; the difference was significant ($F_{1,404} = 4.18$; $p < 0.05$). The mean number of anal rays for the northern subpopulation was 0.39 fewer than that for the southern subpopulation, which was highly significant ($F_{1,379} = 14.33$; $p < 0.001$). Central and southern subpopulations differed by 0.19 rays, which was not significant ($F_{1,373} = 2.93$; $p < 0.10$).

When we partitioned McHugh's (1951) anal fin ray data into their probable subpopulations on the basis of locality, we found his mean anal fin ray count for the combined northern subpopulation samples to be only 0.03 fewer than ours. His southern subpopulation mean ray count was only 0.16 fewer than ours, but, as with vertebrae, there was a large difference in the central subpopulation, with his mean count being 0.36 greater than ours (Table 9).

TABLE 9. Mean Numbers of Anal Fin Rays From McHugh (1951, Table 11, 12 and 13) Compared with Those of This Study: N = Number, $\bar{x}$ = Mean

		McHugh (1951)				This study
		Adult males	*Adult females*	*Young*	*Combined total*	*Combined total*
Northern subpopulation						
	N	105	87	105	297	206
	$\bar{x}$	22.21	21.94	22.28	22.16	22.19
Central subpopulation						
	N	284	418	404	1,106	200
	$\bar{x}$	22.81	22.66	22.79	22.75	22.39
Southern subpopulation						
	N	41	49	100	190	175
	$\bar{x}$	22.83	22.55	22.18	22.42	22.58

Dorsal Fin Rays

McHugh (1951) noted a probable sexual dimorphism in mean dorsal fin ray counts; males had a grand mean difference of 0.12 count greater than that of females. Males in our samples averaged fewer dorsal rays that did females in both northern and southern subpopulations but more rays than did females in the central subpopulation (Table 8). Since the differences between the sexes were not significant and were not consistent in direction, we concluded that the variations were random and we might combine the data for males and females when comparing the three subpopulations.

Central subpopulation anchovies had the largest mean number of dorsal fin rays, 0.09 greater than that of the northern stock and 0.04 greater than that of the southern stock, but these differences are not significant (northern vs. central: $F_{1,904} = 2.27$, $p > 0.10$; northern vs. southern: $F_{1,384} = 0.83$, $p > 0.25$; central vs. southern: $F_{1,378} = 0.33$, $p > 0.25$).

SUMMARY AND CONCLUSION

We found three distinct subpopulations of northern anchovies inhabiting the coastal waters between Newport, Oregon and the southern end of Baja California, Mexico: northern, between Newport and Monterey; central, between San Francisco and lat 29° N and southern, south of; lat 29° N. There was an overlap of about 70 nautical miles for the northern and central subpopulations (Figure 3). Our conclusion was based on our transferrin electrophoresis study, and supports McHugh's (1951) conclusion of three subpopulations. Our morphometric and meristic work also supports our genetic findings.

Given a sample of anchovies from the southern subpopulation range, our studies showed that it could be identified as such if the mean head length, snout length, and eye diameter were greater than those of the northern and central subpopulations, and if the mean standard length of the sample (at all ages) were signficantly less than that of the other two subpopulations. A sample of anchovies from the northern subpopulation range could be identified as such if it had i) a greater mean number of vertebrae and fewer anal fin rays than either central or southern subpopulation anchovies, and ii) if the mean head depth were greater than that of central subpopulation anchovies. However, any conclusion on subpopulations involving meristic counts should take into consideration McHugh's (1951) work showing a high degree of variability in these parameters from year to year and even from month to month.

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THE EFFECT OF THE BOTTOM ON THE FAST START OF FLATFISH *CITHARICHTHYS STIGMAEUS*

P. W. Webb[1]

ABSTRACT

Fast starts of the speckled sanddab, *Citharichthys stigmaeus*, were initiated by a 1 volt per centimeter direct current electric shock and recorded on movie film at 250 frames per second. Observations on kinematics and performance were made for fast starts of fish accelerating in the water column and from a grid located at a distance of 0, 1, 3, or 6 cm above the true bottom. During acceleration the body was bent into a U-shape relative to the bottom. The body sustained a direct push against the grid when accelerating from that grid. The amplitude of propulsive movements of fish accelerating from the grid was larger than acceleration movements of fish in the water column away from the bottom, because the potential for energy wastage due to recoil of the body was prevented by the grid. The distance between the grid and the bottom had no effect on fast starts, ruling out any hydrodynamic ground effect. Motion of fish accelerating in the water column was continuous and predominantly in the horizontal plane. There was little motion of fish accelerating from the grid until they started pushing against that grid. Motion was predominantly in the vertical plane. The resultant distance traveled by fish accelerating from the grid, measured at the end of the principal acceleration period exceeded that of fish accelerating in the water column. Velocities and acceleration rates were highest for fish accelerating from the grid. It was concluded that contact with the sea bottom would enhance fast-start performance of flatfish.

Fish of the order Pleuronectiformes are unique because the adults lie on one side. The habit of inclining to one side is common among other benthic fish that are normally vertically oriented, but no other group shows the specialized morphological adaptations of flatfish. Various observations on benthic fish suggest that inclining the body or lying on one side is advantageous for camouflage and crypsis (Norman 1966). Large locomotor advantages could also accrue, especially to flatfish orienting their body axis parallel to the ground.

Improvements in locomotor performance of flatfish could occur through two mechanisms: hydrodynamic ground effect and pushing against a rigid substrate. The hydrodynamic ground effect occurs through interaction of the downwash from propulsive surfaces with the ground (i.e., the sea bottom) and increases effective thrust and decreases effective drag (Bramwell 1976; Lighthill 1979). It has been described for birds (Withers and Timko 1977) and for pectoral fin propulsion of the mandarin fish, *Synchropus picturatus* (Blake 1979). Pushing against the substrate is obviously more energy efficient than pushing against water because more muscle power is converted into body motion rather than wasted in accelerating fluid. It is utilized by macrurous decapods (Webb 1979). The relative importance and effectiveness of these mechanisms will depend on how flatfish move their bodies near the ground.

The following experiments were performed to determine if the sea bottom could influence fast-start (acceleration) movements and performance of a typical flatfish. Emphasis was placed on fast starts because of their importance in evasion of predators and in catching elusive prey (Eaton and Bombardieri 1978; Webb and Skadsen 1980).

METHODS

Fish

Speckled sanddab, *Citharichthys stigmaeus* Jordan and Gilbert (family Bothidae) were used. Fish were caught in dip nets by divers along the southern California coast, hence avoiding the damage typical of trawl-caught specimens. Fish were held in a 60,000 l tank at 14° C. They were fed twice a week on frozen brine shrimp.

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Procedures

Individual speckled sanddabs were starved for 24 h. Each fish was lightly anesthetized (MS-222)[2] and a white thread was sewn above the center of mass of the stretched-straight body calculated from previous measurements on a subsample of fish. This reference facilitated later film analysis. Each fish was then placed in an observation arena and allowed to recover for 24 h overnight.

The observation arena consisted of a chamber 45 cm long, 30 cm wide, and 40 cm deep. A fast start is a short duration stereotyped activity during which fish travel short distances but accelerate at high rates to reach large speeds (Eaton et al. 1977; Webb 1978). The size of the arena would not interfere with fast-start activity but would prevent sustained high-speed swimming. This study is concerned only with the former activity.

The observation chamber had a false bottom made from a wire grid (2.5 cm squares made from 0.08 cm diameter wire). A solid bottom was located beneath the grid and could be set 0, 1, 3, or 6 cm beneath. Comparison of performance during fast starts with the grid set at various distances above the solid bottom was expected to show the importance of the hydrodynamic ground effect as differences in performances once physical contact with the grid had ended. Vertical reinforcers prevented the grid from acting as a spring when a force was applied by an accelerating fish. The observation chamber also allowed room for fish to swim in the water column for short distances permitting observation of fast starts in the water column remote from all possible ground interaction.

The bottom was located in one of the four positions beneath the grid while the sanddab became accustomed to the chamber overnight. Next morning a 1.0 V/cm d.c. electric shock was used to initiate a fast start either from the grid or when the sanddab was temporarily stationary in the water column clear of the grid and bottom. All experiments were performed at 14° C.

Fast starts were recorded on movie film at 250 frames/s. A 45° mirror above the observation chamber allowed simultaneous observation of top and bottom views. A floating lid prevented surface ripples distorting the top-view image.

Each fish was killed after an experiment. The body outline was traced on paper. Mass, total length, wetted surface area, location of the center of mass, and muscle mass were measured as described by Webb (1977).

There were no differences in these morphometric characteristics among various groups of speckled sanddabs. Combined values were (mean ±2 SE); mass, 28.96±3.78 g; length, 13.7±0.6 cm; the center of mass, located 5.2±0.2 cm from the nose; wetted surface area, 120±10 cm^2; muscle mass, free of skin and scales, 11.78±2.28 g.

Movie film was analyzed frame by frame to observe kinematics and to measure performance. Details are given by Webb (1978). Briefly, performance was measured for the motion of the center of mass of the stretched-straight body. This point approximates the instantaneous center of mass of the flexing body which is the point about which propulsive forces act. Coordinates for motion of the center of mass were measured in the horizontal and vertical planes. The resultant motion of the center of mass was calculated. Velocities and acceleration rates for these three motions (horizontal, vertical, and resultant) were calculated using moving point linear regression methods. Performance parameters were compared using the *t*-test, and significant differences between means are declared at the 5% level.

RESULTS

Kinematics

There were no differences in kinematics of fish accelerating from the grid set at various distances above the solid bottom. Fast-start kinematics for acceleration from the grids (Figure 1) showed the normal three stages originally described by Weihs (1973). During stage 1, the body was bent into a U-posture (0-80 ms in Figure 1A) comparable to the C-posture of other teleosts when viewed from above (Eaton et al. 1977; Webb 1978). The center of mass showed some recoil (i.e., lateral movement in the opposite direction to the tail, and normal to the fish axis) towards the grid because the fish adopted a posture with the body raised by the median fins before a fast start (Stickney et al. 1973). The body was always bent away from the bottom.

During stage 2 (80-120 ms in Figure 1A), the body was bent in the direction opposite to that of stage 1 as the body curvature traveled caudally along the body. Some point of the body remained in contact with the grid almost to the end of stage 2.

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[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

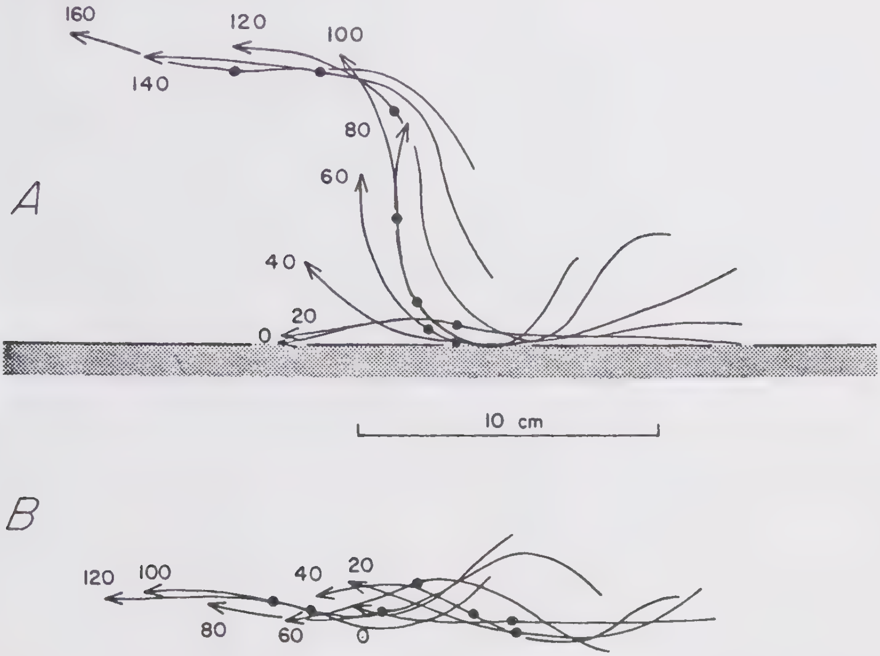

FIGURE 1.—Tracings of the body center-line (seen from the side) at 20 ms intervals to show the acceleration movements during fast starts of *Citharichthys stigmaeus*: A) Acceleration from contact with the grid. B) Acceleration in the water column. Dots show the location of the center of mass of the stretched-straight body. The extended and variable stage 3 following the major acceleration strokes has been omitted for clarity.

The center of mass was propelled vertically away from the ground.

Fast start stage 3, occurring after the major acceleration period, was variable, ranging from an unpowered glide to continued swimming with caudal propagation of propulsive waves sustained from the starting curvature in stage 2.

A typical fast start of a sanddab in the water column away from the bottom is illustrated in Figure 1B. Fast starts in the water column showed the same stages as fast starts from the grid. The amplitude of body movements was usually smaller than those of fish accelerating from the grid. Center of mass recoil, reduced during acceleration from the grid, was observed for fish accelerating in the water column, as seen in other teleosts.

The timing of various fast-start events was similar among groups of fish (Table 1). The duration of stage 1 showed a slight but nonsignificant tendency to decrease as the distance between the grid and the solid bottom increased. The fish accelerating from the grid lost contact after 112 ms, before the completion of stage 2 in 124 ms (Table 1).

Fast-Start Performance

The distance between the solid bottom and the grid had no significant effect on vertical and horizontal distances traveled by the center of mass of speckled sanddabs during fast starts (Figure 2) including distances traveled after losing contact with the grid. This showed that no measurable

TABLE 1.—Results for the duration of fast-start events for *Citharichthys stigmaeus* accelerating from a grid at various distances above a solid bottom and accelerating in the water column. Mean ±2 SE are shown, $n = 10$.

Timing	Acceleration in the water column	Distance between the grid and the solid bottom (cm)				Combined data for acceleration from the grid
		0	1	3	6	
Duration of stage 1, ms	58±8	65±6	65±14	62±8	60±8	63±5
Duration of stages 1 plus 2, ms	105±12	136±18	118±13	149±40	113±9	124±7
Time to end of ground contact, ms	—	116±19	108±9	116±15	113±9	112±6

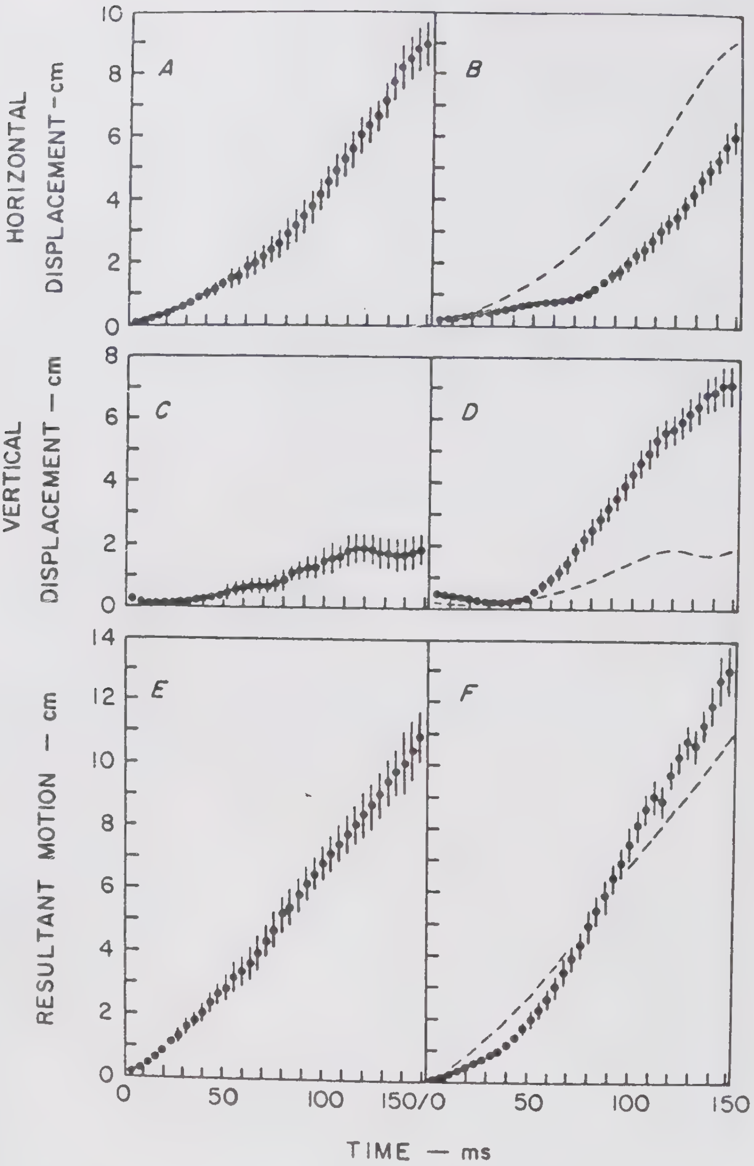

FIGURE 2.—Relationships between the distance traveled by the center of mass (the point about which propulsive forces act) and elapsed time during fast starts of *Citharichthys stigmaeus*. The motion of the center of mass was resolved into the distance traveled in the horizontal (A, B) and vertical (C, D) planes. These data were used to calculate the resultant distance traveled (E, F). Fast-start performance is shown for fish accelerating in the water column (A, C, E) and from the grid (B, D, F). The dotted lines in B, D, and F show the motions of the center of mass of fish accelerating in the water column from A, C, and E to facilitate comparison with fast starts from the grid. Vertical bars shown ±2 SE.

hydrodynamic ground effect influenced speckled sanddab fast starts. All data for fish accelerating from the grid were therefore combined for subsequent analysis and for comparison with fish accelerating in the water column.

The performance of fish accelerating from the grid differed from that of fish accelerating in the water column. The differences were seen in horizontal and vertical motions and in the net (resultant) motion. In the horizontal plane, fish accelerating from the grid traveled 0.8±0.2 cm in 63 ms at the end of stage 1, compared with 1.9±0.4 cm in the same time for fish accelerating in the water column. By the end of stage 2 fish starting from the grid had moved forward 3.9±0.9 cm in 124 ms. This was an improvement over stage 1, but still less than that of fish in the water column which moved forward 6.8±0.9 cm in the same time. The small initial displacement of fish in contact with the grid was probably due to frictional interactions between the fish and the grid (Arnold and Weihs 1978). The normal force at the point of contact would also have been augmented by recoil forces generated by the tail and head tending to displace the fish downwards.

The motion of the center of mass in the vertical plane also differed between speckled sanddabs accelerating from the grid and in the water column (Figure 2C, D). For fish accelerating from the grid there was little vertical movement during fast-start stage 1 because of the presence of that grid. During stage 2, however, the center of mass was accelerated vertically upwards moving 6.0±2.4 cm in 124 ms. Fish accelerating in the water column showed little vertical motion, except that due to recoil (Figure 2C).

The resultant motion of the center of mass of the fish showed differences between acceleration in the water column and from the grid, but these differences were less marked than motions in the horizontal and vertical planes (Figure 2E, F). The increase in distance covered with time was initially greater for fish accelerating in the water column. They traveled a total of 3.7±0.6 cm in 63 ms compared with 2.9±0.4 cm for fish accelerating from the grid. However, once fish pushed against the grid in stage 2, performance improved. By the end of stage 2, they had traveled a cumulative distance of 10.2±1.2 cm in 124 ms, greater than that of 8.7±1.3 cm achieved by fish accelerating in the water column.

Velocities calculated for the center of mass reached maximum values close to the end of stage 2. Maximum values were significantly greater for fish accelerating from the grid compared with fish accelerating in the water column (Table 2). Mean acceleration rates would, of course, follow similar trends to velocities. Maximum acceleration rates only showed significantly improved performance for resultant motion of fish accelerating from the grid (Table 2).

TABLE 2.—Results of maximum acceleration rates and maximum velocities for *Citharichthys stigmaeus* accelerating from the grid and in the water column. Data (mean ±2 SE; $n = 10$) are shown for motion of the center of mass.

Item	Fast starts from the grid	Fast starts in the water column
Maximum acceleration rates, m/s^2:		
Horizontal	37±7	48±10
Vertical	54±10	44±9
Resultant	66±12	46±12
Maximum velocities, m/s:		
Horizontal	66±11	92±10
Vertical	92±12	17±4
Resultant	104±17	76±14

DISCUSSION

These experiments show that the bottom (grid) does influence fast starts in speckled sanddabs. Fast starts from the bottom were associated with large amplitude motions that would normally cause substantial recoil of the center of mass because the bottom prevents that recoil. Motions of fish accelerating from bottom contact were predominantly vertical compared with horizontal motions of fish accelerating in the water column. The relative magnitude of vertical and horizontal displacements of sanddab accelerating from the grid are comparable with those observed in crayfish under similar circumstances (Webb 1979). For both speckled sanddab and crayfish the marked vertical motion is caused by prolonged contact between the body and the ground. Unfortunately, these large vertical displacements in speckled sanddabs preclude any significant hydrodynamic interaction with the ground after contact is lost.

Withers and Timko (1977) give a succinct explanation of this hydrodynamic ground effect, where the ground influences the flow, increasing lift (thrust) and decreasing drag. Hydrodynamic ground effect rapidly declines as the ratio, y/s, increases, where y is the gap between the surface generating thrust and the ground, and s is the span (width) of that surface. Blake (1979) found that 80-90% of the ground effect vanished by the time y/s reached unity in hovering mandarin fish. The mean maximum span of speckled sanddab, located at the center of mass, was 6.7±0.2 cm. For this span, $y/s = 1$ after about 130 ms, 18 ms after the end of physical contact with the bottom (Figure 2D). The caudal fin had a maximum span of 2.4±0.3 cm, and a value of $y/s = 1$ is reached within about 16 ms after the tail loses contact with the bottom (Figure 1A). Thus, the vertical acceleration rapidly lifts the speckled sanddab out of the hydrodynamic influence of the ground so that there is insufficient time for any interaction to affect performance. However, the absence of this effect during a fast start does not preclude hydrodynamic ground interactions from improving steady swimming close to the sea floor.

Thus, the observations on fast starts of speckled sanddab from the bottom show that a single kinematic pattern is used, which sustains bottom contact for most of a fast start, but which prevents development of any significant hydrodynamic ground effect. However, a direct push against a solid substrate will always convert more muscle energy into body motion than working against a fluid. It therefore appears that speckled sanddab utilizes fast-start behavior that makes the greatest use of the available ground interaction options.

However, the interaction with the ground cannot be assumed to be adaptive before considering the question of advantages and disadvantages. For example, the small initial displacement of the center of mass of fish accelerating from the ground might be disadvantageous in some circumstances, such as escaping from predators. However, significant protection is achieved by camouflage and cryptic behavior in pleuronectiform fishes, rendering this contingency unlikely.

The influence of the bottom is clearly advantageous in the capture of elusive prey, a second behavior in which fast starts play a key role (Eaton and Bombardieri 1978; Webb and Skadsen 1980). Elusive prey, e.g., fish and crustacea, are common dietary items for pleuronectiform fishes in the families Psettodidae, Bothidae, and Pleuronectidae (Liem and Scott 1966; Norman 1966). The bottom eliminates recoil so that the fish can rapidly accelerate the head vertically (Figure 1). Continued rapid vertical acceleration is facilitated by prolonged bottom contact through the major acceleration period of a fast start. Bottom contact also results in the acquisition of a superior final speed that would be advantageous in a continued attack. The time taken to accelerate from the bottom and reach maximum speed could also be reduced by resting in sand in a curved U-shaped posture. This may occur since flatfish often dig into sand with the eyes and tail at the surface, but the body buried, implying a curved posture (Hobson 1979). Thus, the morphology and behavior of the benthic sanddab appear to be adaptive in improving fast-start performance, as well as for camouflage. Such advantages undoubtedly apply equally to other members of the pleuronectiformes and therefore provide an additional functional explanation of the unique flatfish body form and habits.

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RESPONSES OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, LARVAE TO PREDATION BY A BITING PLANKTIVORE, *AMPHIPRION PERCULA*

P. W. WEBB[1]

ABSTRACT

Responses of northern anchovy larvae, ranging from 0.29 to 1.2 cm total length, to attacks by a biting planktivore, the clown fish, were recorded on video tape. Schlieren optics were used to simultaneously view an opaque predator and transparent prey. All fish were reared, and experiments performed, at 20° C. The percentage of larvae responding to attacks increased from about 9% for 0.29 cm larvae to 80% for 1.2 cm larvae. Of these larvae responding to attack, 26 ± 10% attempted to escape too late and were caught. This proportion was not related to larval size. The direction of larval escape paths to the initial orientation of the body was not related to larval size, but escape distances traveled and mean escape speeds increased with size from 1.0 cm and 4.0 cm/s respectively for larvae 0.29 cm total length to 3.5 cm and 8.2 cm/s in larvae 1.2 cm total length. Larval performance was not maximal except during rare chases which occurred in 7% of attacks by the predator.

Escape maneuvers in vertebrates are initiated by the magnifying retinal image of an approaching object, called the looming effect, and calculated as the rate of change of the angle subtended by the predator as seen by the prey. In the present study, apparent looming thresholds for larval avoidance responses were calculated at the start of the response, and differ from the true response because there must be a finite time difference between the stimulus exceeding the response threshold and the motor response itself (response latency). Maximum likelihood mean apparent looming thresholds were calculated for log-transformed data, assuming nonresponding prey had apparent looming thresholds greater than the maximum actually observed. These mean apparent looming thresholds decreased with larval length from approximately 32 rads/s at 0.29 cm to 1.7 rads/s at 1.2 cm. The most important feature of the larval avoidance response was that an escape attempt should be made appropriately timed to an attack.

The method could be used to examine larval fish responses in other interactions where predation events take place over a small distance. Examples are attacks by biting juvenile and adult fish, and other planktonic invertebrate predators. Effects of larval density and alternate prey species could also be evaluated.

Predation and starvation are believed to be the dominant factors contributing to the extensive mortality of fish eggs and larvae (Blaxter 1969; Hunter 1977, in press; Hunter and Kimbrell 1981). Following Hjort's critical period concept concerned with the importance of first-feeding success to larval survival (Hjort 1914), most attention has concentrated on feeding behavior and food consumption (e.g., Hunter 1972, in press; Arthur 1976; Lasker 1978). Fish eggs and larvae are also extremely vulnerable to a wide variety of fish and invertebrate predators. A few experimental studies have determined feeding rates for invertebrate predators on eggs and larvae in the laboratory (Lillelund and Lasker 1971; Theilacker and Lasker 1974; von Westernhagen and Rosenthal 1976) and rates of egg cannibalism by fish in the field (Hunter and Kimbrell 1981). I know of no studies that have examined responses of larvae to a fish predator.

Northern anchovy, *Engraulis mordax*, larvae are exposed to a wide range of juveniles and adults of fish and consequently to a range of feeding habits on a continuum from filter-feeding to biting (e.g., Leong and O'Connell 1969). The purpose of the experiment described here was to develop a method to study responses of northern anchovy larvae to attacks by fish, and to determine how avoidance responses and larval vulnerability to capture change during early development. A biting fish planktivore was used as a predator in an attempt to complement studies relating to filter-feeding predators, often crudely simulated by towed plankton nets (e.g., Webb and Corolla 1981).

METHODS

Northern anchovy larvae were reared from eggs

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as described by Hunter (1976). Eggs were spawned from five groups of adults taken from laboratory stocks on five occasions during spring 1980 (Table 1.) Eggs were transferred to noncirculated filtered sea water in 400 l black fiber glass tanks. Food for larvae was the dinoflagellate *Gymnodinium splendens* for 2- to 5-d-old larvae, and the rotifer *Brachionus plicatilis* for older larvae. Water temperature was maintained at 20° C. Larvae were held under constant illumination of 2,000 lx at the water surface, provided by standard room fluorescent lights.

Observations were made on predation of eggs and 10 groups of larvae of different total lengths, ranging from 0.29 to 1.2 cm (Table 1). Lengths were based on measurements of a subsample from each group at the time they were used for experiments. Observations were concentrated on early larvae because this is the period of greatest morphogenesis (O'Connell 1981) and maturation of response systems (Kimmel 1972; Webb and Corolla 1981).

TABLE 1.—Total length of subsample ($\overline{X} \pm 2$ SE; $N = 10$) of northern anchovy larvae populations used in predation experiments with a model predator, the clown fish. Data are also given on spawnings.

Total length at test (cm)		Group	Date spawned (1980)	Date tested
Eggs[1]		C	13 Mar.	13 Mar.
Larvae	0.287 ± 0.015	C	13 Mar.	14 Mar.
	.322 ± 0.008	E	4 Apr.	5 Apr.
	.391 ± 0.020	E	4 Apr.	6 Apr.
	399 ± 0.010	E	4 Apr.	7 Apr.
	.417 ± 0.011	E	4 Apr.	8 Apr.
	.421 ± 0.011	B	28 Feb.	4 Mar.
	626 ± 0.050	B	28 Feb.	12 Mar.
	867 ± 0.053	D	27 Mar.	14 Apr.
	.953 ± 0.090	A	7 Feb.	29 Feb.
	1.166 ± 0.095	A	7 Feb.	18 Mar.

[1] Eggs were 0.135 ± 0.005 cm long × 0.069 ± 0.003 cm wide.

Attempts to obtain natural predators of uniform and suitable size were not successful. Therefore a mimic for biting predators was used. This model was the clown fish, *Amphiprion percula*, cultured from eggs. The fish were held in 40 l polypropylene tanks at 20° C and under constant illumination. The fish were fed daily on a diet of Tetramin[2] and northern anchovy eggs and larvae. The predator was readily available at uniform sizes throughout the duration of the experiment. The clown fish were 4.4 ± 0.2 cm total length (TL) and mass was 1.58 ± 0.17 g. The maximum depth was 1.8 ± 0.2 cm, and maximum width 0.6 ± 0.1 cm, both located 1.3 ± 0.1 cm from the nose (data are $\overline{X} \pm 2$ SE; $N = 10$).

Interactions between the model predator and northern anchovy eggs and larvae were observed using schlieren optics (Holder and North 1963). Briefly, a vertical collimated light beam was produced by a high intensity monochromatic point source at the focus of a concave mirror (focal length 140 cm) attached to the ceiling. A second mirror, with the same focal length, was located at the floor and focused the light on a black spot on a glass plate.

The observation arena was a cylindrical tank, located in the light beam. It was 35 cm in diameter and 10 cm deep and had a plate-glass bottom. The tank contained a central cylinder, 26.5 cm in diameter and 5 cm deep, which supported a circular plate-glass lid. The lid and the bottom were parallel to each other and normal to the light beam. Discontinuities in refractive index (i.e., larvae in the water) deflected the light from the focus spot on the glass plate, and were seen as bright objects against a dark background. Opaque objects (i.e., the predator) were seen as black silhouettes.

The clown fish were starved for 5 d to ensure uniform high motivation. This was necessary because northern anchovy larvae grow rapidly and loss of a day required starting new batches, particularly for young larvae. Individual clown fish were placed in the observation arena and left for 24 h. After this period, up to 100 northern anchovy eggs and larvae were introduced through a side port in the central cylinder. After 10 to 30 min, the predator began feeding on the prey distributed through the tank. The reason for the delay in the onset of feeding is not known. Behavior was recorded on video tape. Experiments were performed at 20° C.

The video tape was manually advanced to analyze images frame by frame (framing rate = 60 Hz). The following observations were made: the number of attacks by clown fish, escape attempts by prey, escape success of the prey, catch success of the predator, and the number of predator errors. The prey escape angle, distance traveled, and mean speed during an escape attempt were measured.

Animals from a wide range of taxa, including fish, show avoidance responses to approaching, presumably threatening objects (see Gibson 1980). The image of such an object on the retina expands rapidly and this magnification in time is called the "looming effect." It is measured as the rate of change of the angle, α, subtended by the approaching object measured at the prey's eye (Dill 1974a, b). The looming effect is greater as the speed of an approaching object increases, as the object gets closer, and for larger objects. The threshold was calculated at the start of an escape attempt by the larvae, after Dill (1974a),

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[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

$$\frac{d\alpha}{dt} = \frac{4\,U S_h}{4(D + d)^2 + {S_h}^2} \qquad (1)$$

where U = predator speed at the time of the prey response,
S_h = predator shape; mean of maximum depth and width of the clown fish,
D = distance between the predator's nose and the prey when the prey responded,
d = posterior distance of the predator's maximum depth and width from its nose.

Here, $d\alpha/dt$ at the start of the response by the larvae is called the apparent looming threshold (ALT). This is because the true threshold must occur prior to the observed motor response because there is a finite delay in the nervous system between receipt of the stimulus and the start of the motor response. The value of this response latency, or reaction time, is unknown for northern anchovy larvae.

RESULTS

Clown fish fed discontinuously on eggs and larvae, feeding intensely on prey in one location and then swimming around the tank before feeding again. Thus the clown fish did not attack prey as encountered, and often ignored nearest prey between feeding bouts. The clown fish were continuously active, swimming mainly by paddling movements of the pectoral fins supplemented with caudal fin beats. The mean speed was 3.2 ± 0.5 cm/s ($\overline{X} \pm 2$ SE; N = 100; range 0.5 to 9.1 cm/s).

Attacks were made on individual larva. Orientation by the clown fish prior to a strike could not be distinguished with confidence from normal swimming. Prey that did not attempt to escape were always caught, with the exception of eggs and the smallest larvae tested. Thus 12% of strikes on eggs and 3% of strikes on nonresponding 0.29 cm larvae were not successful. Predator failures are presumed due to predator error, which has been reported as 8% for largemouth bass, *Micropterus salmoides*, (Nyberg 1971) and 34% for chain pickerel, *Esox niger* (Rand and Lauder 1981). Larvae that made an avoidance response to an attack by clown fish were rarely pursued because clown fish usually attacked another larva. Eight chases were observed in 113 escape attempts by northern anchovy larvae. One escape each was observed for larvae in the 0.626 and 1.166 cm TL groups and two in each of the 0.399, 0.867, and 0.953 cm groups.

Larval responses to attacks by clown fish were characteristic startle responses, followed by a short period of sprint swimming. The startle response consisted of a C-start form of a fast start and a turn (Eaton et al. 1977). The sprint was a period of swimming at constant speed for <1 s (see Hoar and Randall (1978) for definitions). Together, these two components constitute a swimming burst (Webb and Corolla 1981).

The proportion of larvae responding to attacks increased with size, from approximately 9% for 0.29 cm larvae to 80% for 1.2 cm larvae (Figure 1A). The proportion of larvae escaping an attack similarly increased with size, but at a lower rate than the proportion making an escape attempt (Figure 1B). This was because 26 ± 10% (N = 10 groups of larvae) of larvae showing an escape response were eaten anyway, before a chase began. These larvae were defined as attempting to escape too late. This proportion of escaping larvae caught

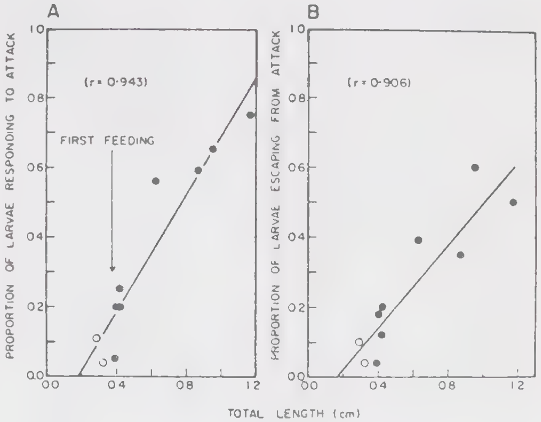

FIGURE 1.—Relationships between (A) the proportion of northern anchovy larvae responding to an attack by clown fish and (B) the proportion escaping an attack, both as functions of the total length. Circles are for prefeeding yolk-sac larvae

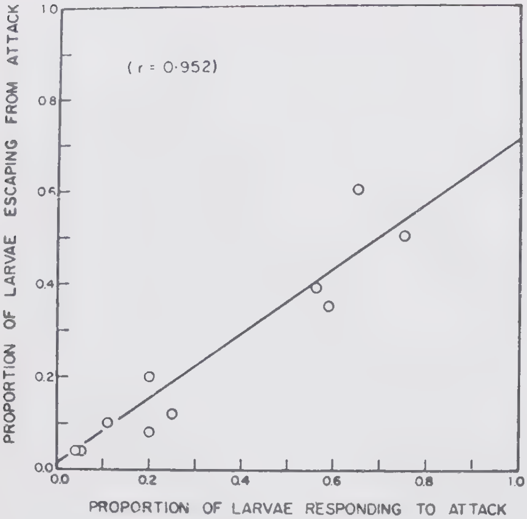

FIGURE 2.—The relationship between the proportion of northern anchovy larvae responding to an attack and the proportion escaping an attack by clown fish.

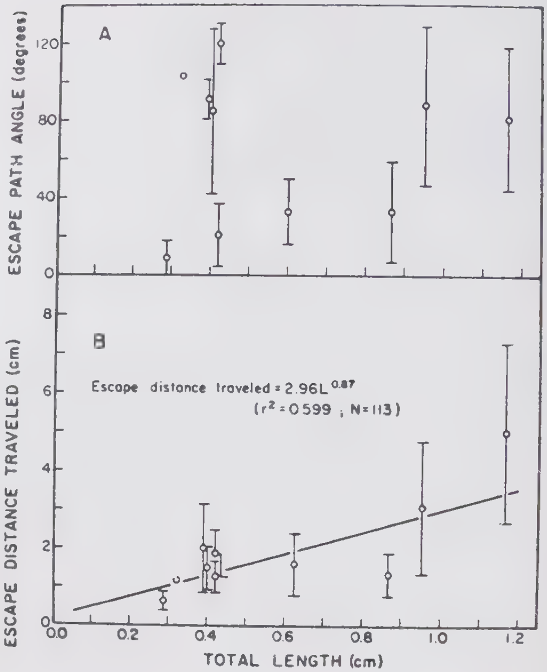

FIGURE 3.—The relationship between (A) the angle of the prey escape path to the predator's strike path and (B) escape distance traveled both as functions of total length of northern anchovy larvae attacked by clown fish. Vertical bars show ±2 SE.

by the clown fish was not correlated with larval size.

The proportion of larvae attempting to escape was therefore related to the proportion escaping (Figure 2). Using functional regression analysis (see Ricker 1979), the relationship was found to be linear, and gave a value of 30% of larvae attempting to escape being captured. This is within the expected range obtained from observations on each group of larvae.

The startle response included a turn. The angle of the prey escape path relative to the predator strike path showed no particular relationship with larval length (Figure 3A), but this was primarily due to the large angles measured for the 0.391, 0.399, and 0.421 cm larvae. Without these data, the escape angle would have increased with larval length, implying larger larvae were better at avoiding the predator's strike path. However, larvae in the three length classes with large angles did not differ from others in any obvious way, and therefore the data cannot be rejected.

However, the distance traveled in an escape swimming burst increased with larval total length (Figure 3B). Using regression analysis (type II) the relationship was best described by a power function, but r^2 values were relatively low. Mean escape speeds in an escape swimming burst also increased with larval size (Figure 4). These speeds were normally about half the mean burst speeds obtained in a forced swimming burst (Webb and Corolla 1981), but escape speeds comparable with the forced maximum were seen during chases.

Analysis of ALT's for larval escape responses is somewhat complex. These ALT's were assumed to be distributed in the population like any other character. However, not all larvae responded. Since nonrespondants were eaten before responding they were assumed to have higher ALT's than larvae showing escape responses. Therefore, the true distribution of ALT's in the population is not known as values above some observed level are missing. Such a population is said to be censored, and since values are missing from one end of the distribution only, it is said to be singly censored. Cohen (1961) has described methods to calculate the maximum likelihood mean and variance of such censored samples. However, before this can be done, the nature of the ALT distribution must be considered.

The nature of the distribution of ALT's in the population was evaluated using probit analysis, developed to examine related problems in toxicology (Sprague 1969). ALT values were ranked and

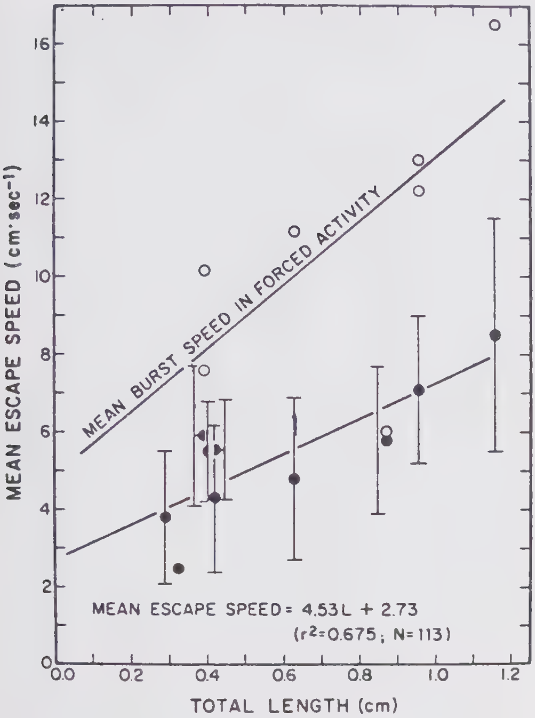

FIGURE 4.—The relationship (dots) between mean escape speed and total length of northern anchovy larvae attacked by clown fish. Vertical bars are ±2 SE. Circles show mean escape speeds during chases. The line for mean burst speeds was taken from Webb and Corolla (1981).

the cumulative percentage of observations was plotted on a probit scale against these values. A logarithmic transformation of ALT values linearized the relationship to the greatest extent (Figure 5) implying ALT's were log-normally distributed in the population. Some curvature remained after this transformation, probably due to decision errors (Treisman 1975) and individual variability in response latencies. Thus ALT values were assumed to be log-normally distributed in the larval populations sampled, and maximum likelihood means and variances were calculated for a type I singly censored sample (Table 2) as described by Cohen (1961). Resulting mean ALT's are shown as a function of total length in Figure 6.

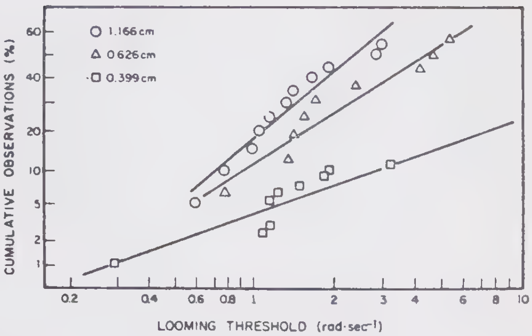

FIGURE 5.—Representative relationships between cumulative number of startle responses, expressed as percentages of total attacks (probit scale) and the logarithm of ALT's for northern anchovy larvae of three different total lengths.

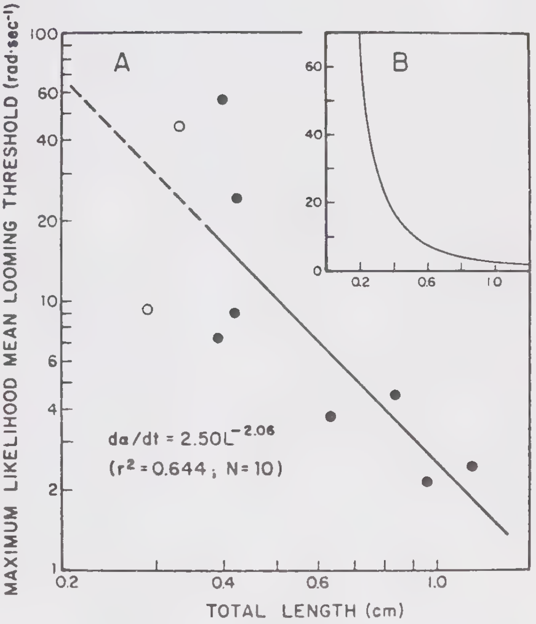

FIGURE 6.—The relationship between the maximum likelihood mean ALT and total length of northern anchovy larvae attacked by clown fish. The relationship is shown for logarithmic coordinates in (A) and for arithmetic coordinates in the inset (B). Circles are for prefeeding yolk-sac larvae.

The most important result from this analysis was that ALT's decreased rapidly with increasing size, and hence development, tending towards a plateau for larger larvae and presumably for adults. The relationship was best described by a power function with a negative exponent (see Figure 6) but such a description should be treated with caution. This is because the ALT distributions were severely censored, with a resulting large variance about each mean. In addition, the residual curvature in the transformed data could influence mean ALT values, but this would not alter the general shape of the inverse relationship between ALT's and larval size.

TABLE 2.—Parameters used in the calculation of maximum likelihood values of the population mean $d\alpha/dt$ (μ) and variance (σ^2) for northern anchovy larvae responses to clown fish predators, using the method of Cohen (1961). Logarithm-transformed data for $d\alpha/dt$ were used in these calculations. $\hat{\lambda}$ taken from tables in Cohen (1961); $h = (N - n)/N$, $\hat{\gamma} = S^2/(\bar{X} - X_0)^2$, $\hat{\mu} = \bar{X} + \hat{\gamma}(\bar{X} - X_0)$, and $\hat{\sigma}^2 = S^2 + \hat{\gamma}(\bar{X} - X_0)^2$.

Length (cm)	Sample mean $\bar{X}$ (log rad/s)	Sample variance S^2 –	Sample range $(\bar{X} - X_0)$ –	h –	$\hat{\gamma}$ –	$\hat{\lambda}$ –	$\hat{\mu}$ (log rads/s)	$\hat{\sigma}^2$ –	N
0.29	0.12	0.03	0.24	0.91	0.56	3.60	0.97	0.23	63
.32	.34	.19	.31	.96	2.00	4.31	1.65	.59	45
39	–.64	.41	–.64	.93	.99	4.18	86	.95	56
40	.10	.08	.52	.87	.30	3.16	1.75	.93	79
42	.17	.11	.36	.75	.87	2.23	.96	.39	32
42	– 05	.07	.41	.91	.42	3.53	1.39	65	45
63	.33	.08	.44	.45	.47	.76	.65	.22	36
83	–.08	.41	63	50	.40	.96	.58	.36	34
95	–.12	.45	.30	.41	.47	.72	.33	.46	40
1.17	.14	.44	.42	42	.46	83	39	.12	32

DISCUSSION

These experiments were performed to examine responses of northern anchovy larvae to attacks by biting (i.e., nonfilter-feeding) fish planktivores such as juvenile fish preying on zooplankters. The nature of the predator is relatively unimportant. Inexperienced larvae are likely to respond to an attack in the same way because in all cases failure to do so is terminal. The other alternative is that prey have specific predator images to which they respond, which seems improbable.

One objective was to evaluate an experimental technique that could be easily repeated and applied further (e.g., to problems of larval vulnerability and starvation interactions, effects of alternate prey species, prey density, and other questions affecting larval predation mortality). For this reason it was considered important initially to use a predator that was readily available at a uniform size. Natural fish predators could not be obtained in good condition and in a reasonable size range for the period of the experiment. Clown fish were found to be an excellent substitute.

However, experiments were performed at 20° C which is at the upper extreme of the temperature range of northern anchovy, but this probably had a small effect on the observations. The energy required for the short periods of high level activity in an escape swimming burst is undoubtedly derived mainly from anaerobic metabolism, which is known to be less dependent on temperature than aerobic metabolism (see, e.g., Bennett 1980). Experimental data on burst swimming performance are only available for rainbow trout and these data confirm the small effect of temperature in the range of 10° to 25° C (Webb 1978).

Two primary measures of response to attack were obtained, the proportion of larvae showing a startle response and the apparent looming threshold for that response. The proportion of larvae responding to attack increased linearly with length (Figure 1). This result is surprising. Kimmel (1972) has shown that several days are required for the Mauthner cell, which initiates the startle response, to extend caudally. The eyes are not functional before first feeding, so they could not initiate a startle response (O'Connell 1981). Neuromasts are present from hatching but if they were involved in stimulating a startle response, very high percentages of early larvae should show responses to attack. These developmental events suggest a rapid increase in percent response to attack would be expected in the yolk-sac stages, approaching maximum response levels at about first feeding, as found for responses to electric shock stimuli (Webb and Corolla 1981).

However, development rates are likely to vary widely in a population of larvae. It is for this reason that food is first added on the second day after hatching in spite of the fact that the mean time to first feeding is about 4 d (Hunter 1976). The percentage of yolk-sac larvae responding to attack was quite small and was probably due to early maturation (most likely of the visual system) of the most rapidly developing individuals.

The ALT changed with larval size, decreasing rapidly as larvae grew in length. This decline could have been due to improved acuity in the visual system and/or maturation of neural pathways processing visual information. This later could include shorter response latencies with age. The changes in ALT may be the basis for the increasing proportion of avoidance responses in larger larvae.

The only other measurement of looming thresholds for fish are those of Dill (1974a, b) for postlarval zebra danio, *Brachydanio rerio*, in response to attacks by largemouth bass and to silhouettes. These data are not fully comparable with those obtained here for several reasons. First, the mean depth plus width was used to characterize the shape of the clown fish. Dill (1974a) used only width, citing reports that fish are more sensitive to horizontal movement than to vertical movement (Cronly-Dillon 1964; Jacobson and Gaze 1964). In contrast, operant conditioning experiments show that fish are particularly sensitive to apices (e.g., Hinde 1970; Baerends 1971) which occur at the dorsal and ventral margins of laterally compressed bodies. In the absence of definitive experiments relating shape to looming response thresholds, the mean value of depth plus width was considered most appropriate. Use of the mean value of depth and width would give larger values of $d\alpha/dt$ than use of depth alone (Equation (1)).

Second, the distance between the nose and the maximum depth and width of the predator was added to the reaction distance separating the predator and prey. This assumes that the prey either has depth vision or sees the equivalent of a silhouette of the predator. The inclusion of this term would reduce values of $d\alpha/dt$ compared with Dill's method.

The ALT values for postlarval zebra danios (2.0 cm long) was 0.43 rad/s. Northern anchovy larvae of the same size would be expected to have a mean value of about 0.6 rad/s from the relationship in Figure 6.

The overall function of the startle response is to avoid predators. How effective is it? The clown fish rarely pursued escaping larvae, although when they did so, the larvae were easily caught. In these experiments, chases may have been rare because larval densities were high. However, observations on adult piscivores attacking single prey show that chases are also rare with pike, *Esox* (Neill and Cullen 1974; Webb and Skadsen 1980), largemouth bass (Nyberg 1971; P. W. Webb unpubl. obs.), and rock bass, *Ambloplites rupestris* (P. W. Webb unpubl. obs.). Presumably the cost of pursuit is large relative to the benefits of capturing small prey particularly where there are alternative prey. In a normal planktonic assemblage, alternate prey could be important in reducing vulnerability of larval northern anchovy, especially in the presence of more opaque forms and those with more strongly pigmented eyes (Zaret and Kerfoot 1975).

Unfortunately, there are no field observations on larval responses to predation, and the likelihood of making the requisite field observations is remote. Nevertheless, the response of a prey to an attack is an obvious indicator of the prey's awareness and the possible difficulty of capture. The reluctance of many predators to attack responding prey, as noted above, together with the behavior of the clown fish observed in these experiments, imply that the startle response is an effective deterrent. Thus, it is most important that the larvae respond, but initially maximum swimming speeds are not required. Indeed the latter would be energetically more costly. Larvae clearly behave appropriately with a submaximal evasion (Figure 4), except when maximum performance becomes desirable in the rare event of a chase. Nevertheless, timing of the escape attempt must be accurate as 24 to 30% of the larvae attempted a response too late to escape capture.

Larval looming response thresholds will not only be important in escaping biting predators, but also other predation threats. Webb and Corolla (1981) discussed relationships between burst swimming performance of northern anchovy larvae and escape probabilities from plankton nets as a crude analogy with filter-feeding predators. While swimming performance could explain a large part of net avoidance, other factors were involved. Webb and Corolla suggested that declining response thresholds with experience would be important so that larger larvae responded earlier to an impending collision. The inverse relation between ALT with larval total length suggests that such changes occur. Presumably, similar thresholds or size relations would apply to larger predators. Then the reaction distance to a net moving, for example, at a given towing speed would be expected to be greater for larger northern anchovy larvae. This would contribute significantly to the size-dependent sampling bias of such nets.

This work has attempted to evaluate a method for quantifying responses of a fish larva to attacks by a predator as one step in studying the neglected aspect of predation on larval mortality. The advantages of the method are the visualization of both opaque and transparent individuals of small size and continuously recording their behavior. The disadvantages are that the space viewed must be small and hence only small predators can be used, and filtering predators are excluded. However, predation could be studied for particular feeders (e.g., biting fish and chaetognaths) arthropods (e.g., copepods and euphausids), and less discriminating feeders such as thaliaceans and cnidarians. These are abundant in the plankton. In addition, effects of 1) larval density, 2) alternate prey in mixed planktonic assemblages, and 3) effects of starvation on larval vulnerability to predation could be studied.

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BURST SWIMMING PERFORMANCE OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, LARVAE

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ABSTRACT

Burst swimming performance was measured for northern anchovy larvae from 0.23 to 1.33 cm total length at a temperature of 17° C. Fast starts and burst swimming were initiated using a 3 V/cm direct current electric shock. Performance was measured from movie film recorded at 250 frames/s. Percentages of larvae responding to the stimulus increased from 9% 40 hours after eggs were spawned to a maximum of 95±4% after 125 hours. Distances traveled in a given time period increased linearly with length so that maximum speed ($U_{\max}$) and mean speed ($\bar{U}$) similarly increased linearly with total length (L) according to $U_{\max} = 20.8\ L + 1.95$; $\bar{U} = 8.18\ L + 4.89$. The maximum distance traveled per burst ($S_{\max}$) was used as a measure of endurance and increased with length according to $S_{\max} = 3.79\ L + 0.08$. These swimming speeds and endurance relationships can explain a large portion of size-dependent selectivity of towed plankton nets.

Larval swimming performance has been the focus of several studies (Blaxter 1969; Rosenthal and Hempel 1970; Hunter 1972). These have emphasized sustained swimming speeds which are considered an important factor affecting the volume of water searched by a larva, and hence food density requirements or the encounter frequency with food items. These low levels of activity apparently affect ration and at the same time are major contributors to routine energy expenditures (Vlymen 1974).

In contrast, very high activity levels (fast starts and steady burst swimming) are rare. While they are unlikely to constitute a large metabolic load, high speeds are essential to the act of capturing food items (Hunter 1972) and in escaping from predators. This aspect of larval performance has not been evaluated. Therefore, the purpose of this work was to determine the effect of size on burst swimming performance (acceleration and sprints) for northern anchovy, *Engraulis mordax*, larvae, and to evaluate the importance of such high levels of activity in prey capture and escape from predators, including nets.

METHODS

Northern anchovy larvae were reared from eggs as described by Hunter (1976). Eggs were spawned from five groups of parents taken from laboratory stocks on five separate occasions during the fall of 1979 (Table 1). Eggs were transferred to noncirculated filtered seawater in 400 l black fiber glass tanks. Food for the larvae was the dinoflagellate *Gymnodinium splendens* for 2- to 5-d-old larvae, and thereafter the rotifer *Brachionus plicatilis*. Water temperature was maintained at 17° C. Larvae were held under constant illumination from standard room fluorescent lights.

Experiments were performed on larvae of 11 different total lengths, ranging from 0.23 to 1.33 cm. Observations were concentrated on larvae in the first few days after hatching (Table 1) when greatest larval development occurs (O'Connell in press).

Groups of 5-50 larvae were observed using Schlieren optics. Details of this system are given in Holder and North (1963). Briefly, a vertical collimated light beam was produced by a high intensity monochromatic point source at the focus of a concave mirror attached to the ceiling. A second mirror on the floor focused the light on a black spot on a glass plate. The focal length of the mirrors was 140 cm.

A cylindrical tank, 17 cm in diameter and 5 cm deep, with parallel plate glass top and bottom, was introduced into the light beam. Discontinuities in

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TABLE 1.—Summary of spawning batches and dates of anchovy larvae of various total lengths used in experiments on burst swimming performance. Data for total length are $X \pm 2$ SE.

Total length (cm)	Batch of eggs[1]	Date spawned (1979)	Number of larvae sampled
0.23±0.03	E	2 Dec.	10
0.27±0.03	B	1 Nov.	10
0.29±0.02	B	1 Nov.	10
0 34±0.05	E	2 Dec.	10
0.46±0.03	C	8 Nov.	10
0.51±0.05	C	8 Nov.	10
0 55±0.06	A	31 Oct.	10
0.65±0.06	A	31 Oct.	10
0.72±0.04	C	8 Nov.	5
1.14±0.08	C	8 Nov.	5
1.33±0.27	A	31 Oct.	5

[1] Batch D was infected by bacteria and therefore rejected

the refractive index (e.g., larvae in water) deflected the light from the focus spot on the glass plate and were seen as bright spots against a dark background.

The stimulus initiating a maximum fast start and swimming burst was a 10 ms, 3 V/cm square wave electric shock delivered via two grids in the water bath. Responses were recorded on Kodak[3] Plus-X 16 mm movie film at a framing rate of 250 Hz. Experiments were performed at 17° C.

Movie film was analyzed frame by frame. The progression of the head was traced from frame to frame and the mean distance travelled was calculated as described by Hunter (1972) avoiding artifacts due to lateral oscillations of the head associated with propulsive movements. Speeds were calculated from the distances travelled and the elapsed time between measurements. Elapsed time was calculated from the product of number of frames between measurements divided by the framing rate.

RESULTS

The percentage of larvae responding to the nonspecific electric shock stimulus increased with age to a maximum of 88-100% (mean 95±4%; n = 7) after 125 h measured from the time of spawning (Figure 1). This corresponds to the age at which larvae raised under the same conditions begin intermittent swimming, i.e., periods of low speed swimming alternating with periods of rest (Hunter 1972).

The response to the stimulus was a fast start followed by a period of continuous high speed (sprint) swimming. Fast starts and sprint speeds are defined as burst activities (see Webb 1975; Hoar and Randall 1978 for definitions). Therefore the response can be described as a burst of swimming activity.

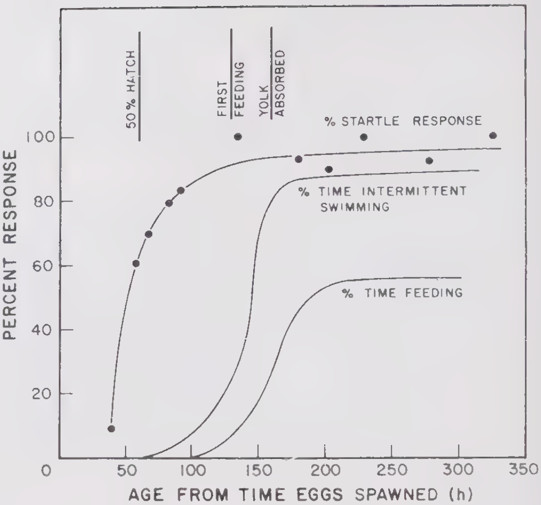

FIGURE 1.—Percentage responses (n = 20-50) to a 3 V/cm d.c. electric shock by northern anchovy larvae as a function of age, calculated from the time the eggs were spawned. The curve was fitted by eye. The curves for the time spent in intermittent swimming and in feeding are from Hunter (1972).

Kinematics of larval fast starts and sprint swimming have been described in detail for zebra danio, *Brachydanio rerio*, (Eaton et al. 1977) and for northern anchovy (Hunter 1972). No differences were seen in the present experiments and therefore details are not repeated.

The most direct, and hence most accurate, measure of performance during a burst of swimming is the distance traveled in a known elapsed time for larvae accelerating from rest. The form of this relationship for the distance traveled by larvae of various total lengths is shown in Figure 2 for three representative time periods. Data were described by best fit linear regression equations without data transformation (Table 2). Similar linear relationships have been shown for larval cruising performance of plaice, *Pleuronectes platessa*, (Ryland 1963); herring, *Clupea harengus*, (Rosenthal 1968); walleye, *Stizostedion vitreum vitreum*, and yellow perch, *Perca flavescens* (Houde 1969). The total distance traveled per burst of swimming (S) also increased linearly with total length (L) according to

$$S = 0.08 + 3.79 \pm 0.76 L \quad (r^2 = 0.57; n = 85).$$

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[3] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

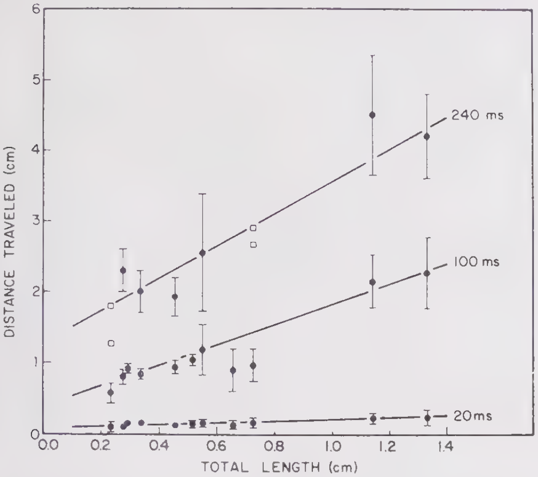

FIGURE 2.—Exemplary relationships between the distance traveled and total length of northern anchovy larvae after 20, 100, and 240 ms of burst swimming initiated by an electric shock stimulus. Vertical bars show ± 2 SE. Open squares show individual data points for individuals of groups of larvae when few swam for 240 ms.

TABLE 2.—Summary of relationships between distance traveled (S in centimeters) in various elapsed times as functions of total length (TL in centimeters) of northern anchovy larvae stimulated to maximum performance by an electric shock. 95% confidence intervals about the slope are shown.

Elapsed time from start of swimming (ms)	Best-fit equation relating distance traveled with total length	r^2	n
20	$S = 0.09 + 0.10 \pm 0.04$ TL	0.31	95
40	$S = 0.15 + 0.37 \pm 0.08$ TL	0.65	95
60	$S = 0.17 + 0.80 \pm 0.15$ TL	0.67	87
80	$S = 0.21 + 1.17 \pm 0.22$ TL	0.68	83
100	$S = 0.28 + 1.46 \pm 0.27$ TL	0.71	81
140	$S = 0.54 + 1.75 \pm 0.37$ TL	0.69	65
180	$S = 0.82 + 2.06 \pm 0.44$ TL	0.75	48
220	$S = 1.07 + 2.25 \pm 0.60$ TL	0.73	36
260	$S = 1.26 + 2.52 \pm 0.53$ TL	0.66	23

These distances were traveled by continuous swimming because gliding is limited for organisms the size of the larvae moving at low speeds (see Weihs 1980).

Although the relationships between distances traveled and total length were best described by linear regression equations, the coefficients of determination indicated that the relationship usually described only 65 to 75% of the variability. A major contributor to the variability was the apparent low performance of larvae with mean total lengths of 0.65 and 0.72 cm. For example, r^2 for the relationship between distance traveled in 100 ms and total length increased from 0.71 to 0.83 on deletion of the observations for larvae in these two groups. However, the larvae appeared healthy and there were no apparent reasons to assume these data were anomalous. The reason for their lower performance is unclear. Another factor contributing to variability in the data may have been the use of larvae from several spawnings at different times from different small sets of only 25-50 parents from laboratory stock. The very low r^2 for the distance-total length relationships at small elapsed times can also be attributed in part to greater measurement error. Larvae traveled small distances, of the order of 1 mm in 20 ms for small fish, and even with magnification of 2× these small distances were obviously subject to greater measurement error than larger distances.

Swimming speeds were not constant. Speed increased with time to reach the maximum burst speed after 80-100 ms and then speed declined for the remainder of the burst (Figure 3). The time to reach maximum burst speed was not affected by total length, but the decrease in speed from the maximum was greater for larger larvae, and extended over a longer period of time. The maximum burst speed increased linearly with total length (Figure 4), and since time to maximum speed was independent of length, mean acceleration rates will also be proportional to total length. Mean speeds during a burst of swimming ($\overline{U}$) also increased linearly with length (Figure 5), but at a lower rate than maximum burst speeds ($U_{\max}$) where

$$\overline{U} = 4.89 + 8.18 \pm 1.1\,L \quad (r^2 = 0.861;\ n = 85)$$
$$U_{\max} = 1.95 + 20.8 \pm 2.5\,L \quad (r^2 = 0.891;\ n = 85).$$

The difference between maximum and mean speeds increased with total length because variations in speed in a burst increased with total length (Figure 3). Maximum and mean speeds during a burst were consequently similar for the smallest larvae.

Figure 5 also shows other relationships between swimming speed and length reported in the literature for comparison. The mean speeds measured for anchovy larvae were greater than those measured for other larvae, exceeding the "... theoretical 10 body lengths/sec ..." (Blaxter 1969) maximum. Intermittent swimming speeds (Hunter 1972), the normal voluntary swimming pattern of larvae, and voluntary bursts were lower than the burst speeds measured here, presumably because of the absence of threatening stimuli.

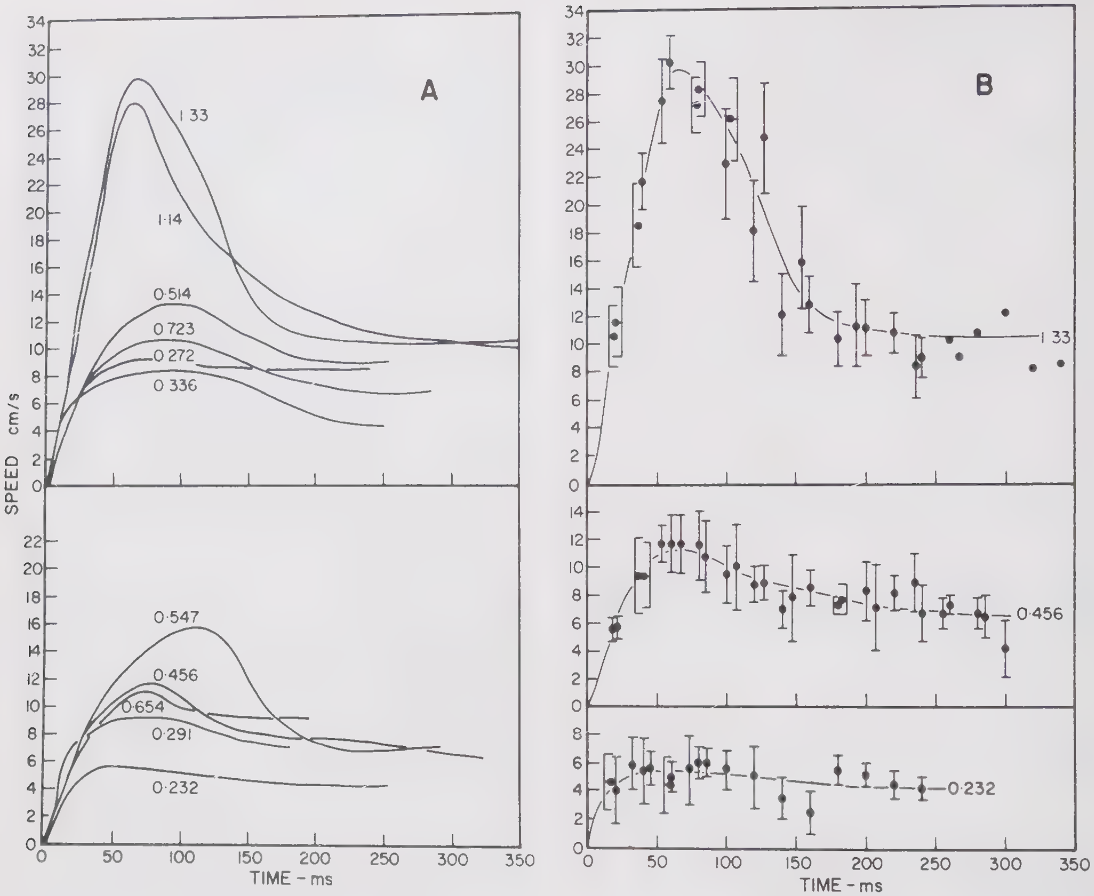

FIGURE 3.—Relationships between swimming speed and time during a burst for 11 groups of northern anchovy larvae ranging in mean total length from 0.23 to 1.33 cm. Panel A shows mean curves, separated into two groups for clarity. Panel B indicates the nature of the data from which the curves were constructed. Curves were fitted by eye. Vertical bars show ± 2 SE.

DISCUSSION

Northern anchovy larvae are important planktonic predators as well as being prey items for other organisms. Burst swimming speeds and burst swimming response ability will be important in this predator-prey role because the ability to rapidly strike prey and to escape strikes by predators will make major contributions to survival.

Response ability was assayed following an electric shock stimulus. While this is not a normal stimulus, observations on adult fish suggest responses to electric shock and more typical stimuli are comparable (Eaton et al. 1977; Webb 1978, 1979). For the larval northern anchovy, response patterns to electric shock correlated with expectations based on the onset of intermittent swimming and feeding (Figure 1). Similar patterns of maturation of the nervous system, especially the eyes (O'Connell in press), and reduced vulnerability to predators (Lillelund and Lasker 1971) suggest the stimulus is a suitable assay for maturation of locomotor coordination systems.

Following maturation of response capabilities, the effectiveness of a larva as a predator and in avoiding predation will depend to a large extent on locomotor performance (Lillelund and Lasker 1971). A model by Howland (1974) showed speed and maneuver were major factors in catch and avoidance behavior that contribute to success in predator-prey encounters. Larvae may be pursued

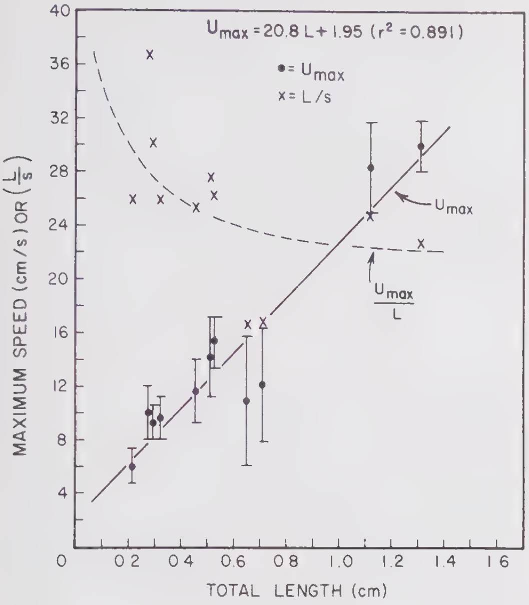

FIGURE 4.—Maximum burst speeds (U_{max}) as a function of total length (L) for northern anchovy larvae. Solid circles are absolute speeds (cm/s). Crosses show specific speeds in body lengths (L/s) calculated as U_{max}/L. Vertical bars show ± 2 SE.

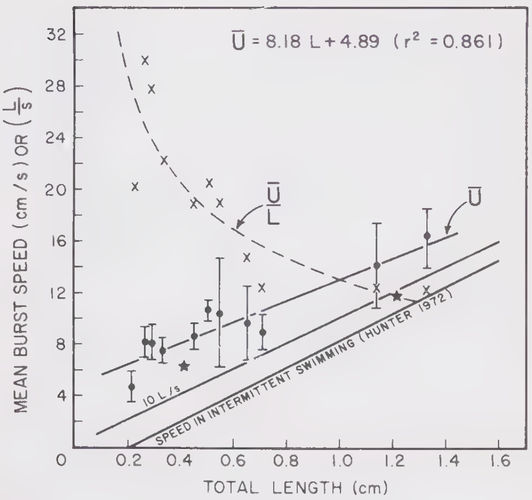

FIGURE 5.—Mean burst speeds ($\bar{U}$) as a function of total length (L) for northern anchovy larvae. Solid circles are absolute speeds (cm/s) and crosses show specific speeds ($\bar{U}$/L). Vertical bars show ± 2 SE. The 10 body length/s relationship is based on Blaxter (1969). The intermittent swimming speed relationship is taken from Hunter (1972). Stars show mean voluntary burst speeds, from Hunter (1972).

by predators so that endurance must be added to these components of predator-prey behavior. Of these three factors the physical ability to turn seems least important. Fish can turn in extremely small radius circles (Webb 1976; Eaton et al. 1977; Kimmel et al. in press) so that the optimal escape strategy of turning inside a predator's turning radius, forcing the predator to stop and reorient (Howland 1974), is probably impractical. For artificial predators, nets, the scale of the net makes turning ability unimportant. Therefore, speed is expected to be the major performance component of larval behavior contributing to the outcome of encounters with their prey, while both speed and endurance will affect interactions with predators and nets.

Hunter (1972) found that northern anchovy larvae accelerated over 8-16 ms to reach their prey. He found that a 0.8 cm larva would travel about 0.04 cm in that time, and a 1.3 cm larva about 0.09 cm. In the present experiments, the distance traveled was 0.03 and 0.09 cm in 12 ms for larvae of 0.8 and 1.3 cm TL, respectively. This shows that northern anchovy larvae use their maximum burst performance in attacking their prey.

Northern anchovy larvae are also prey items for a variety of fish and invertebrates (Hunter 1977, in press) so that the larvae would require a variety of response patterns to attempt to escape from predation. For example, lunging predators typically overshoot the prey location (Hoogland et al. 1956; Hunter 1972) when the rapid acceleration in a fast start would facilitate escape by quickly removing the potential prey from the predator's strike path. The rapid improvement in maximum burst speed with size (Figure 4) should reduce the vulnerability of larger northern anchovy to such predators. Chasing predators, for example, juvenile fish and larvae of more active species such as scombrids, are at the opposite extreme to lunging predators. Northern anchovy larvae should have reduced vulnerability to such predators as they grow because of improved mean swimming speed during a burst (Figure 5). In addition, the distance traveled per burst increases with size, implying improved stamina with increasing total length which should further facilitate escape of larger larvae from chasing predators.

The effect of size on the ability of northern anchovy larvae to escape natural predators and the mechanisms involved in escape behavior have received little attention. Decreased vulnerability of larger larvae to predation by copepods and euphausids has been documented (Lillelund and Lasker 1971; Theilacker and Lasker 1974), but since experiments were performed in the dark, the factors leading to reduced vulnerability are not known. An alternative approach to assessing the importance of changing swimming performance with larval size is to consider an artificial "predator," a net, which simulates some actions of certain natural predators, such as filter feeders. The problem of sampling bias by nets has provided a variety of observations and models suitable to evaluate size-performance effects on vulnerability.

Most studies of net avoidance start with, or parallel, Barkley's (1964) model on selectivity of towed nets. This model identified three factors determining escape (and catch) probabilities: reaction distance, speed, and orientation of the escape path. Endurance must be added. In the absence of adequate data on the relevant parameters for fish larvae, results of sensitivity analyses have been fitted to catch data (Barkley 1964, 1972). The present data can be used to compare scaling relationships between escape probability and burst swimming performance to evaluate the importance of the latter in determining vulnerability of northern anchovy larvae to net "predators." Such a scaling approach allows some simplification because it is reasonable to assume that probability distributions for orientation of escape paths do not scale with size.

Escape probabilities, as a function of length, can be estimated from a comparison between day and night catches using towed nets. The ratio of night/day catches as a function of larval northern anchovy length is well known to be linear (Ahlstrom 1954; Zweifel and Smith in press) which means that the relationship between escape probability and size is curved, rapidly approaching an asymptote (Figure 6). The data shown in Figure 6 were obtained with a 1 m diameter ring net towed obliquely at about 125 cm/s (Zweifel and Smith in press). Ninety percent avoidance is reached by 1.0 cm larvae, with rather small improvements in escape probability at greater lengths. The decline in escape probability cannot be attributed to the capture of starving or sick larvae (Isaacs 1965) because O'Connell (1980) found no emaciated larvae >1 cm TL in net-caught samples.

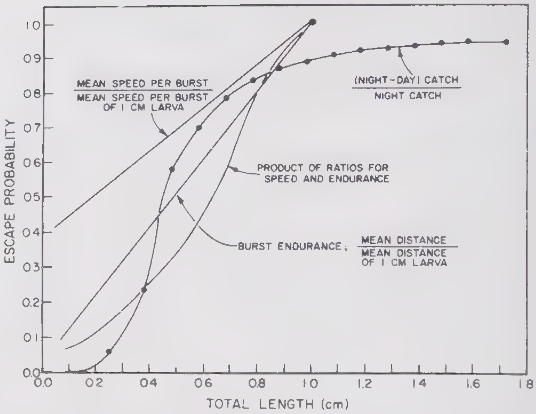

FIGURE 6.—Escape probabilities, estimated from day-night plankton net hauls, and those possible on the basis of burst swimming speed, burst endurance, and their product as a function of total length of northern anchovy larvae. Performance data are normalized with respect to a larval length of 1 cm, where the escape probability reaches 90%. Data for day-night catches were taken from Zweifel and Smith (in press).

In order to compare performance data with the catch probabilities, mean speeds and distances traveled in a burst were normalized about the performance measured for 1 cm larvae (Figure 6). The scaling relationship for mean speeds in a burst, assuming bursts are repeated until a larva escapes, obviously do not parallel escape probabilities (Figure 6). Endurance in a burst shows a greater length effect, which is further accentuated by the interaction (product) of speed and endurance. This latter curve has the steepest slope, most closely paralleling escape probability, such that it is apparent that speed and endurance are major determinants of avoidance ability.

However, the shape of the curves suggests avoidance is underestimated for larger larvae between about 0.4-1.0 cm long. Length dependent maturation of sensory systems and motor control (O'Connell 1980) may contribute to increased escape probability of larger larvae. A behavioral factor may also contribute. Dill (1974) has shown that experienced juvenile zebra danio respond earlier to a predator than do inexperienced fish. Since the predation rate is high for northern anchovy larvae, then larger larvae are likely to be much more experienced with diverse attacks than are smaller larvae. Response thresholds decreased linearly with contacts up to 10 encounters in Dill's experiments, but this effect would undoubtedly decline with larger numbers of encounters, when a minimum threshold would presumably be obtained. Therefore, an age (experience) dependent decrease in reaction distance may contribute to net avoidance and the declining rate of catch probability at larger sizes.

Finally, it should be noted that improvements in plankton nets and catch techniques would shift the position of the curves in Figure 6. This would require different normalization points in evaluating effects of performance on escape probability, taking into account the new point at which larvae out-swim the net. However, such changes would not alter the nature of the arguments nor the conclusions concerning the importance of swimming performance in determining escape probability.

ACKNOWLEDGMENTS

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In all organisms, shape is a real and distinctly biological phenomenon (Bookstein, 1978). Accurately quantified, shape in fishes is important for functional and ecological investigations. For example, Keast and Webb (1966) catalogued feeding and locomotory habits of individual lake fishes and related these to body form, described qualitatively. One could make better inferences of ecology and function from shape if specific aspects of form were isolated, quantified, and then related to function or ecology. Ecologists have also used morphological measurements of birds or lizards (Hespenheide, 1973) and more rarely fishes (Gatz, 1979a, b), as the basis for ecological generalizations about community structure. Such generalizations depend on measurements which accurately decribe functionally important attributes of hape. The system I propose allows these attributes to be more easily isolated and consciously ecombined.

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DIVISION OF LABOR BETWEEN MEDIAN FINS IN SWIMMING DOLPHIN (PISCES: CORYPHAENIDAE).—Two primary components of the propulsive system of a fish are the muscle system and the body surfaces which react with the water to generate thrust. Both of these components show functional variations in relation to activity level. It is well known that the muscle system has two major components of red muscle, a low power, almost inexhaustible system functional at low speeds, and white muscle, a high power, rapidly fatiguing system that provides power at high activity levels (sprint speeds and acceleration). While some overlap in function exists at intermediate speeds, the major function of red and white muscle at different activity levels has led to the concept of a "division of labor" between the two systems (Bone, 1978).

Translation of muscle power into thrust power depends on the way the body moves and the distribution of dorso-ventral depth along the body length; as with muscle, optimum requirements vary with activity. Hydrodynamic theory (Lighthill, 1970; Weihs, 1972, 1973) and experimental observations (Webb, 1977) have shown that a deep tail and small anterior depth and area are optimal for steady (time independent) swimming. The opposite is true for turning and acceleration when body area should be maximized by large depth along the whole body length. In actinopterygians, body shape for these activities can be varied as fish can control the extension of their fins (Bone, 1971; Eaton et al., 1977; Wardle and Reid, 1977; Webb,

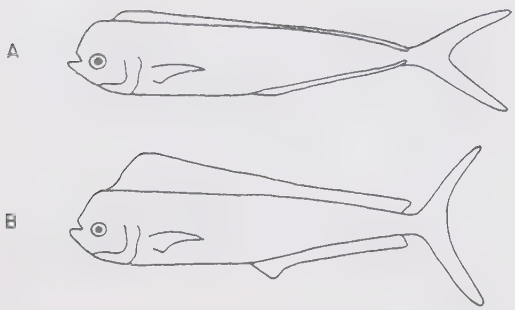

Fig. 1. Tracings from video tapes of dolphin fish showing the use of the median fins A) during steady swimming and B) during acceleration turns.

1977). Changes in the longitudinal distribution of depth and hence area can therefore act as a "variable propeller" optimizing thrust generation according to activity. A logical extension of this variable propeller would be specialization of different median fins for different activities, for which each fin could be more efficient than using a single multiple-function fin. Such specialization could be called a division of labor analogous to that of muscle specialization.

This note reports observations on the dolphin, *Coryphaena hippurus*, which has a lunate tail, usually associated with specialized steadily swimming species (Sharp and Dizon, 1978) and large collapsible dorsal and ventral fins, more appropriate for unsteady swimming (Weihs, 1972, 1973; Webb, 1977). The purpose of the observations was to test the hypothesis that these fins have discrete functions in different activities.

Observations were made in a rectangular tank, 12.7 m long, 4.2 m wide and 4.0 m deep. Water temperature was 22 C. The tank contained dolphin *Coryphaena hippurus*, yellowtail *Seriola dorsalis*, lookdown *Selene vomer*, blue and gold snapper *Lutjanus veridus*, and northern anchovy *Engraulis mordax*. Data were obtained for three dolphins (mean length, L = 1.09 m). Supplemental observations were made on the yellowtails (L = 0.61, N = 10) because this species has a specialized lunate tail and lacks the ability to substantially alter the longitudinal distribution of depth.

The dolphin and yellowtail were captured south of Cape San Lucas, Baja California, using baited hooks and line. At the time of the experiments, the fish had remained in the tank for 11 months. Fish were fed a submaximum ration in three feedings per day. The diet was dead panaeid shrimp, smelt and squid. The fish swam continuously around the tank between feedings. During feeding, the fish swam discontinuously with numerous acceleration turns, combining a sudden rapid acceleration with a turn, to catch food items and to stay in the vicinity of the feeding area.

Video tape recordings were made of steady swimming activity between feedings and of unsteady swimming during feeding. In the former case, only steady swimming in the center of the tank was recorded midway between the ends. Video tape was analyzed using a stop-action recorder. Tape was advanced by hand to resolve events to within $^1/_{60}$ sec (17 msec). The extension of the anterior median and caudal fins were recorded. Specific swimming speeds ($L \cdot sec^{-1}$) were calculated for fish swimming normal to the camera. Turning radii were calculated from the geometry of the camera field and the known lengths of the fishes. The number of tail beats required to negotiate a 180° turn was recorded.

The lunate caudal fin was used for steady low-speed cruising by both dolphin and yellowtail and the long anterior median fins of the dolphin fish were fully furled (Fig. 1A). Dolphins swam in the sub-carangiform mode (more than one-half of a propulsive wave included along the body) and yellowtail swam in the carangiform mode (less than half a wavelength seen). Mean cruising speeds were $0.72 \pm 0.03\ L \cdot sec^{-1}$ ($x \pm 2$ SE; N = 46) for the dolphin and $1.13 \pm 0.06\ L \cdot sec^{-1}$ (N = 20) for the yellowtail, similar to speeds of other fish in the wild (Beamish, 1978).

Unsteady swimming (acceleration turns) was observed during feeding. Dolphins fully extended their median fins immediately prior to a maneuver (Fig. 1A), furling them immediately on completion of the maneuver. They completed a 180° turn in one tail beat. This is comparable with non-lunate tail species, such as trout and goldfish with large fin areas (Weihs, 1972; Webb, 1976, 1977; Eaton et al., 1977). Yellowtail showed few turns and used three tail beats to negotiate a 180° turn. Specific turning radii (turning radius/length) were 0.13 ± 0.01 L for dolphin and 0.23 ± 0.06 L for yellowtail at mean speeds of $1.48 \pm 0.16\ L \cdot sec^{-1}$ (N = 27) and $2.27 \pm 0.34\ L \cdot sec^{-1}$ (N = 12), respectively. Higher speeds were probably prevented by limited space due to the presence of other fish competing for food. The minimum specific turning radius of rainbow trout, *Salmo gairdneri*, an unspecialized non-lunate tail species, has been found to be independent of length with a mean value of 0.17 L (Webb, 1976). Specific turning radii are probably independent of size for other species so that values for fish of different lengths can be used as a basis for comparison. Howland (1974) has suggested that speed and turning radius of fish are inversely related as for rigid bodies. However, when fish flex their bodies to power a turn, the turning radius could be independent from speed or even decrease with increasing speed.

These observations show that dolphin fish use their median fins in distinct ways in steady and unsteady swimming activities consistent with a division of labor among median fins. During steady swimming, the lunate tail is employed alone, similar to specialized lunate-tail swimmers. This would maximize thrust (Lighthill, 1970) without a substantial drag penalty due to a large anterior area (Webb, 1973). However, the efficiency of the lunate tail is probably lower than that of specialized forms because dolphins continue to swim in the subcarangiform mode rather than the more efficient carangiform mode (Lighthill, 1970). This is probably because the body width of dolphin fish is relatively small, promoting flexibility, while the reduced depth of the caudal peduncle (narrow necking) is not as well developed. Thus dolphins retain some kinematic features of steady swimming of non-lunate tail propulsion with some morphological features of specialized lunate-tail swimmers. Dolphins would be expected to be more efficient swimmers than the non-lunate tail species but less efficient than specialized lunate tail forms.

During unsteady acceleration maneuvers, dolphins fully erect their median fins, the same as non-lunate tail species (Eaton et al., 1977; Webb, 1977). This would maximize thrust production for such activities (Weihs, 1972, 1973). However, the lunate tail has a relatively small area compared to non-lunate tails and this would be expected to reduce turning ability to some extent. In practice, the dolphin is able to turn in a smaller circle than trout, a non-lunate tail species. It is probable that the dolphin's thin body could offset possible disadvantages of the lunate tail in powered turns. Certainly the yellowtail, with a short thick body, had considerable difficulties in negotiating a turn.

The division of labor between the lunate tail for cruising and the median fins for acceleration turns reflects the normal habits of the dolphin. Like other lunate tail species, the dolphin is migratory. Dolphins also forage in schools and take elusive pelagic prey similar to other lunate tail species (Kojima, 1961, 1965; Sharp and Dizon, 1978). However, dolphins are usually found in smaller schools and regularly forage under natural and artificial floating rafts of various materials where good maneuverability would be advantageous. Indeed the latter habits are the basis for a lucrative fishery (Kojima, 1965; Hunter and Mitchell, 1968).

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DIEL BEHAVIOR OF THE TIGER SHARK, *GALEOCERDO CUVIER*, AT FRENCH FRIGATE SHOALS, HAWAIIAN ISLANDS.—Adult tiger sharks, *Galeocerdo cuvier*, are among the largest aquatic predators in tropical and subtropical reef communities and are well known for their euryphagic diet (Ikehara, 1960, 1961; Tester, 1969; Fujimoto and Sakuda, 1972; Taylor and Naftel, 1978). However, the majority of information on the daily movement patterns of this shark comes from anecdotal field observations. For example, in Caribbean waters tiger sharks were considered nocturnal because they were rarely observed at the surface during the day but often captured on set lines (Randall, 1967) or encountered near fishing operations (Springer, 1943), at night. While tiger sharks inhabit the tropical waters of Florida throughout the year (Springer, 1963), some individuals migrate northward in the summer months along the western Atlantic coast as far as Woods Hole, Mass. (Bigelow and Schroeder, 1948). Limited data from conventional tagging studies in Hawaiian waters indicate that tiger sharks may restrict movements within a geographic area for at least part of the year (Tester, 1969).

Much still remains to be learned of the diel activity patterns of tiger sharks. Herein, we present results of the first telemetric study on this predator and provide detailed data on the daily spatial requirements of a free-swimming adult tiger shark in its natural environment.

Study area and methods.—French Frigate Shoals is located in the center of the Hawaiian Archipelago, approximately 900 km northwest of Honolulu, Oahu (Fig. 1). The area was chosen because it offered a topography conducive to day and night operations of a small tracking boat and an abundance of sharks. In addition, it lies within the Hawaiian Island National Wildlife Refuge and presents a natural reef ecosystem relatively undisturbed by human activity. The shoal consists of a shallow reef on the north and east (windward) sides with a deeper leeward shelf (approximately 20–40 m deep) that extends westward to the reef drop-off. There are 13 small sand islands scattered on the reef and one basalt island, La Perouse Pinnacle, near the center of the shoal.

A high-power, long-range ultrasonic transmitter was developed to monitor the activity patterns of adult tiger sharks. Tags incorporated a modified version of the circuitry described by Ferrel et al. (1974), and transmitted at frequencies near 32 kHz. The cylindrical package was 25 cm long, 4 cm in diameter and weighed 440 g in air. Pulse intervals were controlled by a resistive depth sensor sensitive from 0 to 140 m and adjusted to rates ranging from 0.5 to 1.5 pulses/second, respectively. Signals were monitored with a tuneable ultrasonic receiver and a staff-mounted directional hydrophone. Absolute maximum range of the transmitter-hydrophone system under ideal conditions was approximately 4,000 m although transmission loss greatly reduced the audible signal at ranges greater than 2,000 m.

Transmitter signals were monitored from a 7-m tracking boat in which bearing and range estimates of the shark were recorded every 15 min. Bearings were taken with an oil-filled navigation compass based on the direction of the strongest audible signal. Accuracy of the bearing estimates was tested and found to be within ±7°. Range estimates were based on the relative

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SWIMMING OF YOLK-SAC LARVAL ANCHOVY (*ENGRAULIS MORDAX*) AS A RESPIRATORY MECHANISM

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Larval anchovy exhibit regular bouts of continuous swimming interspersed with periods of resting during the first 3 days after hatching. At this stage larvae have yolk-sacs and jaws have not developed, so that this behaviour is not related to feeding. Hunter (1972) suggested that this behavior might have a respiratory function. Another explanation is that swimming is required to counter the tendency to sink due to the negative buoyancy of larval anchovy. Possible functions of the swimming bouts are investigated theoretically and experimentally in this study.

Respiration must be by cutaneous diffusion, as the gill system is not developed in yolk-sac larvae. Thus, mathematical models for diffusion to both resting and moving larvae are developed, and predictions by the models are compared to published values of oxygen requirements of anchovy larvae. The models predict that when the oxygen level in sea water is above 60% of saturation, the amount of oxygen diffused to a motionless larva is enough to sustain it. However, at lower oxygen levels, swimming induces convective diffusion and requires an accompanying large increase in the oxygen transport.

Experiments were carried out with newly hatched and 24 h old larvae by placing them in closed containers with a controlled level of oxygen. The behaviour of the larvae placed in water was monitored with oxygen concentrations ranging from saturated to 20% saturation. The number, frequency, duration, and direction of swimming bouts was recorded in each of five oxygen concentrations. The experiments were spread out over a number of weeks to reduce the possibility of bias due to a defective cohort group.

The frequency and duration of swimming periods did not change when the oxygen concentration was reduced from saturation to 80 or 60%. However, as predicted by the diffusion models, increases in the amount of time spent swimming were observed at lower (40 and 20%) concentrations. Time spent swimming increased linearly with the decrease in available oxygen.

Because behaviour of yolk-sac larvae did not change at high oxygen concentrations, swimming activity at or near saturation is not primarily a respiratory act. The second hypothesis, swimming to control depth, was tested by measuring the swimming direction taken by the larvae. For newly hatched larvae, which are approximately neutrally buoyant, no preferred direction was found. However, for 24 h old larvae, an average direction of 39° (measured upwards from the horizontal direction) was found. Day old larvae have used up part of the available yolk and are negatively buoyant. The average distance this larvae sank (>5 cm) was in good agreement with the average distance (<7 cm) moved vertically upwards during one swimming bout. Therefore, it is concluded that swimming activity of yolk-sac anchovy larvae is also related to depth control.

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STALKED EYES AS AN ADAPTATION TOWARDS MORE EFFICIENT FORAGING IN MARINE FISH LARVAE

D. Weihs and H. G. Moser

ABSTRACT

The development of stalked eyes in the larvae of some midwater marine fish species is studied. Our mathematical analysis suggests that this adaptation results in an increase in feeding efficiency.

The larvae of most marine fish species, including benthic ones, live in the upper mixed layer of the ocean where primary and secondary production is high and where competition for the available food particles, as well as the chances of predation on the larvae, are great. The myriad morphological, physiological and behavioral adaptations these larvae have evolved for survival in this environment have only recently begun to be understood (Blaxter, 1974).

Among the more remarkable adaptations are those involving the eye. Larvae of certain groups of midwater salmoniform and myctophiform families have larvae with markedly narrowed, elliptically shaped eyes, and in some of these species the eyes are borne on stalks (Fig. 1, Table 1). The possible significance of narrowed and stalked eyes has not been examined to date. Since they have evolved independently in phylogenetically distinct orders, it seems likely that they are adaptive and it is the purpose of this note to suggest some possible advantages of these adaptations. Stalks vary in length from cases where the medial surface of the eye lies just outside the surface of the head, to quite long, as in the Idiacanthidae where they reach a length greater than ¼ of the body length and are supported by a cartilaginous rod (Brauer, 1908; Beebe, 1934). In bathylagids (Tåning, 1931) and myctophids (Moser and Ahlstrom, 1970; 1974) there is a complete range of conditions from species with round sessile eyes, to species with elliptical sessile eyes, to species with stalks of various lengths. Where the phenomenon occurs in eels (Smith, 1979), the eyes are not on slender stalks but protrude within an envelope of skin and are more appropriately called telescopic. In some species with narrow-eyed larvae (Table 1), particularly in the Myctophidae and Scopelarchidae, a lunate to conical mass of tissue is attached to the ventral surface of the eye. It is part of the chorioid layer of the eye and may function during metamorphosis when the eye must enlarge rapidly and become round (Moser and Ahlstrom, 1970).

The major causes of larval fish mortality are starvation and predation and interactions between them (Hunter, 1976). Feeding and predator avoidance are largely dependent on vision and eye specializations to improve these can therefore be expected. Sighting distance and visual field are major limitations for feeding larvae. Hunter (1972) showed that anchovy larvae notice and strike at food particles positioned within a 60° cone parallel to the body axis with maximum height of about one body length (10 mm). Similar behavior is known for larvae of *Coregonus* and *Esox* (Blaxter and Staines, 1971). As suggested by Moser and Ahlstrom (1970), increase in rotational ability around the long axis of the eye would enlarge the observable volume available from a given point. Extension of the eyes on stalks would further enlarge this volume. This raises the possibility of

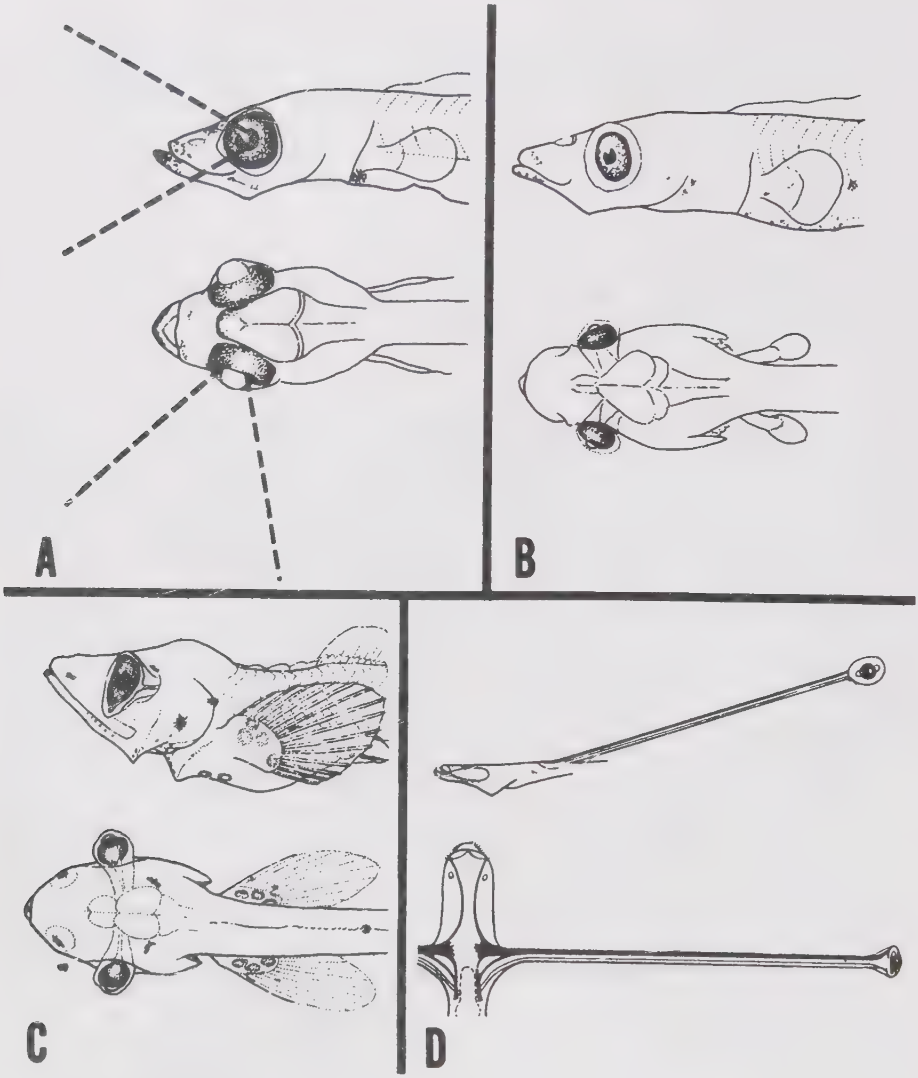

Figure 1. Various eye shapes of marine teleost larvae. A, Round eye—*Bathylagus milleri*, lateral view (above) of 10.6-mm larva; dorsal view (below) of 9.5-mm larva; B, Narrow sessile eye—*Bathylagus wesethi*, lateral view of 8.8-mm larva; dorsal view of 8.5-mm larva; C, Narrow slightly stalked eye of 7.0-mm *Myctophum nitidulum* larva (after Moser and Ahlstrom, 1970); D, Markedly stalked eyes of 16-mm *Idiacanthus fasciola* larva (after Beebe, 1934).

detecting prey from greater distances with a minimum of body motion, thus both conserving energy and reducing the probability of attracting the attention of predators (Lillelund and Lasker, 1971).

We propose that enlargement of the visual field has evolved progressively through several stages. The first stage would be a narrowing of a sessile round

Table 1. Occurrence of elliptical and stalked eyes in larvae of teleost fishes. "+" indicates presence of character in taxon and "++" indicates that the character state is widespread in taxon

Taxon	Elliptical Eyes	Ventral Chorioid Tissue	Stalked Eyes
Anguilliformes			
Congridae	++	+	short
Xenocongridae	++	+	short
Synaphobranchidae	++	0	short
Notacanthiformes	+	+	short
Salmoniformes			
Argentinoidei			
Bathylagidae	++	0	short to long
Stomiatoidei			
Gonostomatidae	+	0	short
Sternoptychidae	++	0	0
Chauliodontidae	+	0	short
Stomiatidae	+	0	short
Astronesthidae	+	0	short
Melanostomiatidae	+	0	short
Malacosteidae	+	0	short
Idiacanthidae	+	0	long
Myctophiformes			
Notosudidae	++	0	0
Myctophidae	++	+	short to long
Evermanellidae	++	+	0
Scopelarchidae	++	+	0
Perciformes			
Labridae	+	+	0
Scaridae	+	+	0

eye. Genera and species with narrow and slightly protruding elliptical eyes (Fig. 1B) are common in all the groups which have stalk-eyed larvae (Table 1). The next stage would be the extension of the eyes on short stalks so that they lie just outside the margin of the head (Fig. 1C). Such an eye could presumably rotate freely, in contrast to a round cup-shaped eye which lies flat in the developing orbit. Numerous examples of such stalked eyes are found in the Bathylagidae, in the stomiatoid families and in the Myctophidae. The final stage, where the eyes are borne on pedunculate stalks of various lengths, is found in the Bathylagidae, Idiacanthidae and Myctophidae (Fig. 1D).

To examine the hypothesis of increased visual field quantitatively, we first assume the visual perception distance d (Fig. 2) to be equivalent in stalked or unstalked eyes. The volume observable, V, by a single unstalked eye is obtained from

$$V = \int_0^{\psi_1}\int_0^{\theta_1}\int_0^{d} r^2 \sin\theta \, dr \, d\theta \, d\psi = \psi_1(1 - \cos\theta_1)\frac{d^3}{3} \quad (1)$$

where r, θ, ψ are spherical coordinates (Moon and Spencer, 1971, or any Vector analysis textbook), and ψ_1, θ_1 are the field cone angles in radians in the azimuthal and vertical directions, respectively. (When $\theta = \pi$ and $\psi = 2\pi$, equation (1) leads to the formula for the sphere volume $V = 4\pi\frac{d^3}{3}$.) For Hunter's (1972) data

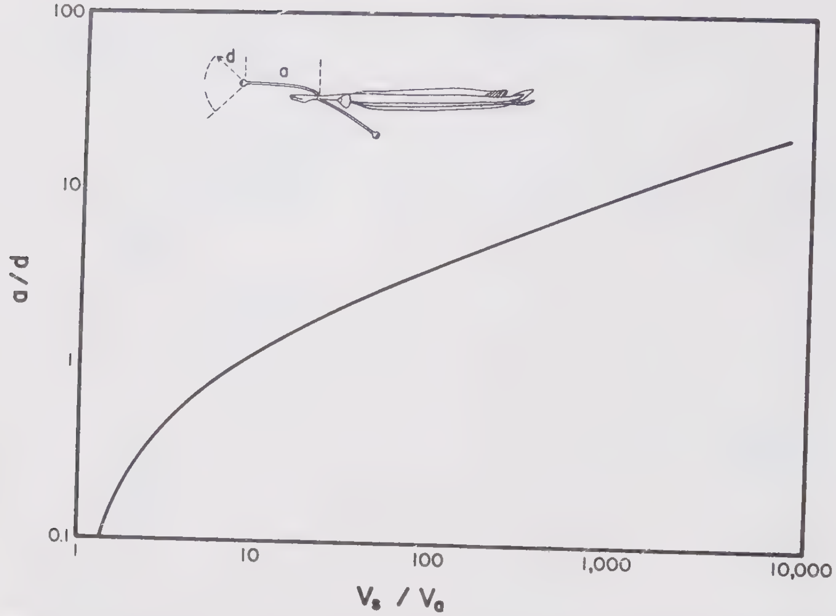

Figure 2. Ratio of the volume sighted by stalked eyes V_s, to that covered by fully rotatable eyes attached to the head V_a, versus the ratio of stalk length a to perception distance d. *Idiacanthus* larva is shown to illustrate the geometrical parameters.

$(\theta_1 = \psi_1 \simeq \frac{\pi}{3})$ the volume covered by both eyes is

$$V = 2\frac{\pi}{3}\left(1 - \frac{1}{2}\right)\frac{d^3}{3} = \frac{\pi}{9}d^3. \qquad (2)$$

The volume is approximately 8% of the volume of the sphere of radius d. Any adaptation towards freely rotatable eyes (as in the chameleon), which enables the volume observed to approach the spherical shape, would be a significant improvement. Improved eye rotation in fish larvae with elliptical eyes seems highly likely, but confirmation must await future field or aquarium observations.

The visual field of larvae with stalks is examined next. In eye stalks of preserved *Idiacanthus* larvae the supporting catilaginous rod is rather stiff but pliable with more flexible hinge points at the attachment to the head and eyeball. The extrinsic eye muscles pass along the posterior surface of the rod and fan out to their points of origin and insertion at either end. The structure suggests that the stalks may be freely waved or flexed and that the eyeball itself may be rotated in two planes to the extent that the larva can look back at itself. With this assumption, if stalk length is a, the volume covered by both eyes V_s is spherical, with radius a + d. This can be compared to the visual volume of fully rotatable eyes with no stalks by writing the ratio of volumes covered

$$\frac{V_s}{V_a} = \frac{4}{3}\pi(a + d)^3/\frac{4}{3}\pi d^3 = \left(1 + \frac{a}{d}\right)^3 \qquad (3)$$

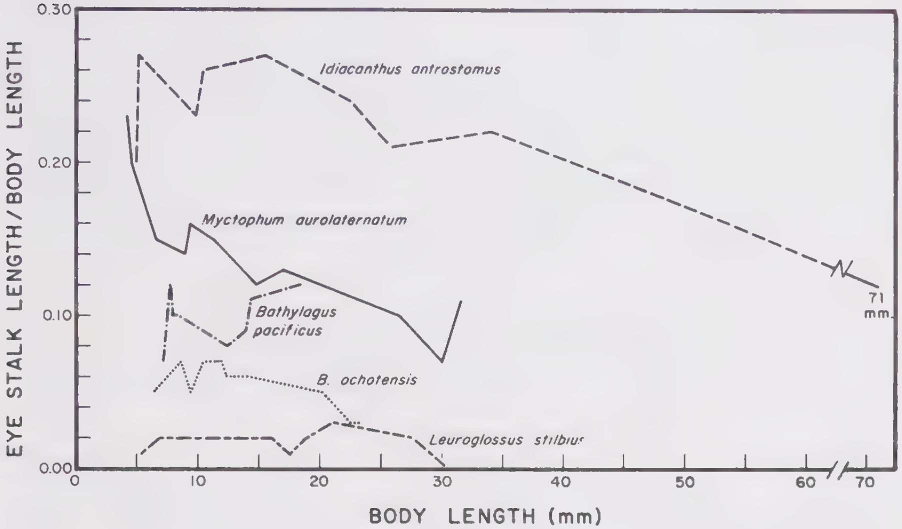

Figure 3. Ratio of eye-stalk length to body length, versus body length for larvae of five species.

The values of this ratio, as a function of a/d are shown in Figure 2. The increase in volume covered is enormous, especially for relatively long stalks (large a/d). The visual perception distance is assumed to be similar for all larvae, so that we can apply Hunter's (1972) perception distances. This distance seems to level off for larvae of more than 12 mm body length with d ≤ 10 mm. We take the maximum value d = 10 mm, since the striking distance for smaller larvae may not be related to perception distance. In any case, this choice is conservative as it results in an underestimate of the increase in visual field due to eye motility. We now combine this with values of a in Figure 3 to obtain the ratio a/d required in Figure 2. For example, *Idiacanthus*, at 44 mm length, had stalks of over 9 mm length, i.e., $\frac{a}{d} \simeq 0.9$ and $\frac{V_s}{V_a} \simeq 7$, so that the total volume covered by this species of stalked larva is over 80 times that of an equivalent larva, i.e., of similar size and optical acuity, with fixed non-rotatable eyes.

This immense increase in observable range, therefore, indicates a potential for a large increase in feeding efficiency, defined as the ratio of energy intake to energy expenditure in finding the food (Weihs, 1975), by increasing the foraging effectiveness. This is a special advantage in areas of low food density, where rather long searches may be required for each prey particle of appropriate size. It is expected that the eyes would be manipulated to follow the prey during the approach stage, so as to decrease the probability of a missed capture.

Eye-stalk motions as an alternative to swimming would also reduce the disturbance to the surrounding water mass, which is a result of the transfer of energy from larvae to the water by viscous drag effects. As a result, pressure signals, which could attract predators (or warn prey), are reduced and the chance for survival is further increased. These advantages are large enough to compensate for the evolutionary investment in the growing of stalks which are resorbed at later stages. Actually, the tenfold increase in sighting volume made possible by just enabling non-stalked eyes to rotate, strengthens our assumption that even narrowed eyes, as in Figure 1B, are shaped for increased searching capability. This results from the observation that the narrow eyes are embedded in a larger hemispherical depression (Fig. 1B) so that the additional space is available for the postulated rotation. The energy required for moving the eyes is much smaller than that of moving the whole body.

Behavioral observations of the types of larvae mentioned here have not been reported. We hope that the present predictions will lead to increased interest and further understanding of these fascinating adaptations.

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in the treatment schedule may be necessary to produce optimum chromosome morphology.

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BODY SECTION VARIATIONS IN SHARKS—AN ADAPTATION FOR EFFICIENT SWIMMING.—Many species of sharks (mainly of the generalized group typified by the carcharhinids and the demersal group, as defined by Thomson and Simanek [1977]) and other pelagic, highly maneuverable fish species such as pike exhibit a curious distribution of body-mass in the longitudinal direction (Fig. 1). The head is compressed vertically to produce a horizontal wedge with rounded edges (roughly elliptical). At around one-quarter to one-third of the total body length the cross-section gradually changes into a rough ellipse with the long axis in the vertical direction (including the first dorsal fin). This configuration is typical of the central and rear part of the fish body, except when approaching the caudal peduncle where horizontal flattening occurs, again resulting in a horizontally elongated cross-section. Another change is observed immediately posterior to the peduncle where the caudal fin is highly elongated in the vertical direction.

The functions of these changes from horizontally elongated to vertically stretched body cross-sections have been speculated on for many years, and Houssay (1912) came up with an ingenious, but incorrect explanation. Due to the scarcity of information on sharks (Gruber and Myrberg, 1977), his reasoning is still widely accepted (Budker, 1971). It is, therefore, the purpose of this note to clarify the fallacy in Houssay's model, and to propose a different mechanism for these adaptations based on recent hydrodynamic analyses of fish locomotion.

Houssay suggested that the alternating elongation is physically equivalent to the shape of a jet of water issuing from an elliptical orifice. Standing waves which result in a periodic change in the shape of the jet are produced by alternating the direction of the long axis of the ellipse. This phenomenon is a result of an interaction of completely different mechanisms—surface tension and inertia of the jet. Surface tension causes the elongated part of the section to move inwards, tending to form a circular section, while the liquid's inertia causes this motion to overshoot resulting in ellipticity in the perpendicular direction. This is therefore a purely dynamic effect of the interface of two fluids,

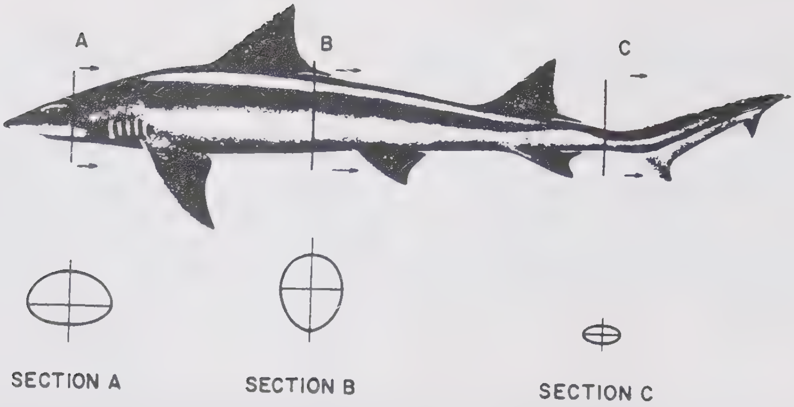

Fig. 1. A "typical" pelagic shark (*Triakis acutipinnae*) showing distribution of oval cross-sections along body.

with no relation at all to the shark's body, which is obviously not liquid. The problem of understanding the advantages of the observed cross-section shape distribution still remained unsolved, therefore.

The effort required for sideways motion of any section of the body is a function of the hydrodynamic resistance and inertia (virtual mass). Both the inertia and form drag are greatly reduced when an elongate section is moved parallel to the longer axis, as compared to moving it in the direction of its short axis, for the same section area.

The intertial effects, known as virtual, or added mass effects which dominate when motion is initiated, are proportional to the square of the largest dimension perpendicular to the direction of motion (Lighthill, 1969; Webb, 1975). Thus, the force required to overcome the inertial reaction to starting a cylinder with elliptical section with a 2:1 aspect ratio (for example) along its large axis (Fig. 2B) is four times smaller than that required to move the same section along its small axis (Fig. 2A). In addition, the hydrodynamic drag experienced after motion is already taking place is much smaller, when the ellipse is moving parallel to its long axis (Fig. 2B). (This is simply shown by moving an object such as your hand through water at constant speed in both orientations.) Here the numerical values of the drag ratio are much more difficult to obtain as they depend on Reynolds number, freestream turbulence and other factors, but these are not required for the present qualitative arguments.

Starting from the anterior parts, we notice that turning maneuvers in fish (Weihs, 1972) start with a rapid motion of the head in the direction of turn. The turning radius is highly dependent on the rate at which this motion is performed. Thus, the decrease in vertical depth of the body section at the head enables a faster turn due to the decreased inertial effects and drag.

Sharks, as well as other species of fish with this body configuration, swim in the anguilliform mode (Breder, 1926). This requires lateral oscillations of the whole body as part of the swimming mode. Here an additional advantage of the vertical compression of the head comes in, as the drag due to side motions while swimming is reduced.

The same arguments, in reverse, hold for the central part of the body. In the turning process (Weihs, 1972), the reaction of the water on the outward motion of this part of the body produces the centripetal force bringing about the actual turning. Increasing the depth of sections in this part will therefore cause a larger reactive force, and therefore a swifter turn with smaller radius. Thus the change in direction of the body eccentricity causes the fish's effort to be applied in the correct place for efficient turning.

In straight line swimming, the lateral compression of the mid-body region helps minimize sideways excursions of this part of the body, which would cause flow separation and in turn increase the resistance to forward motion.

Thickening of the cross-section is again observed at the rear part of the body. This part

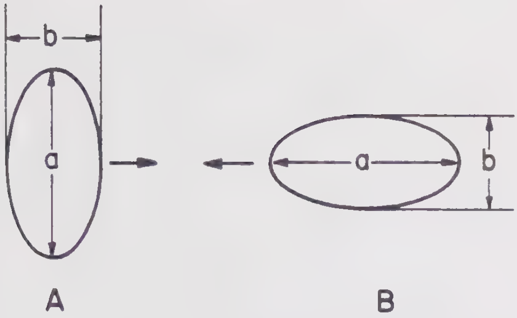

Fig. 2. Motion of an elliptical cylinder of 2:1 aspect ratio normal to (2A) and parallel to its large axis (2B).

of the body is moved sideways with an amplitude increasing to a peak at the caudal peduncle, as part of the anguilliform swimming mode. The larger amplitudes here are needed to drive the caudal fin which in turn provides a large part of the thrust required for swimming. These lateral excursions can therefore not be eliminated but their energetic cost can be reduced to increase efficiency. Again, this is achieved by producing a roughly elliptical section which moves in the direction of its large axis. To further decrease the drag on the peduncle region, some species have developed long appendages on the second dorsal and ventral fins (Fig. 1), or even series of finlets which serve as flow vanes, decreasing the shedding of vorticity and drag (Aleyev, 1977). The horizontal flattening of the peduncle has an additional function (Magnuson, 1970) producing a part of the lift required to counteract negative buoyancy in some species. Finally, the caudal fin is elongated vertically to produce a large, high aspect-ratio hydrofoil propelling the fish by sideways motions. Another adaptation advantageous to rapid maneuvering is the "double tail" produced by the second dorsal and ventral fins, in front of the caudal fin.

In conclusion, the observed changes in body section shape, as a function of distance from the head, help reduce the effort required for maneuvering and cruising. This improvement is in addition to the lateral instability mentioned by Thomson and Simanek (1977) as aiding maneuverability. An increase in mouth ingestion area, and improved stereoscopic vision may well be additional beneficial results of this adaptation.

Acknowledgments.—This note was written while I was NRC-NOAA Senior Research Associate at the NOAA Southwest Fisheries Center, La Jolla. I would like to thank J. R. Hunter and R. Lasker for their hospitality and Ken Raymond for assistance with the graphics.

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VOLUNTARY SWIMMING SPEEDS OF TWO SPECIES OF LARGE CARCHARHINID SHARKS.—The elasmobranchs (sharks, skates and rays) have survived virtually unchanged for hundreds of millions of years, indicating an extremely successful adaptation. Very little information exists, however, on the behavior (Gruber and Myrberg, 1977) of the larger sharks, mainly because of the difficulties of observing these fish in the ocean (Nelson, 1977) and of keeping them under controlled conditions that simulate their life in the wild.

Most pelagic sharks are negatively buoyant (Budker, 1971) and must, for this reason, move continuously to counter their tendency to sink. This motion, which is also applied to seeking

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NOTES

EFFECTS OF SWIMMING PATH CURVATURE ON THE ENERGETICS OF FISH MOTION

Many respiration and other behavioral and physiological studies of larger pelagic fish species are carried out in round tanks (Fry 1957; Bainbridge 1958; Magnuson 1970; Neill et al. 1976). These tanks have structural and space advantages, since round tanks have the largest volume to surface area of any flat-sided enclosure.

However, circular tanks introduce an additional stress factor not usually encountered by wild fish. This is the centripetal force required for continued motion in a curved path. This force is proportional to the fish mass, and inversely proportional to the path radius. The tank radii are limited by the fact that respiration and heat transfer data are obtained from the medium, resulting in a requirement of relatively small volumes so that changes in the measured parameters (oxygen concentration, temperature, etc.) are enhanced.

As will be shown here, this constraint on tank size causes the centripetal contribution to the force balance to become dominant in certain experimental situations. I therefore developed a correction factor to be applied to data collected in round or annular tanks so as to make the data representative of fish swimming freely in a straight line, in open waters.

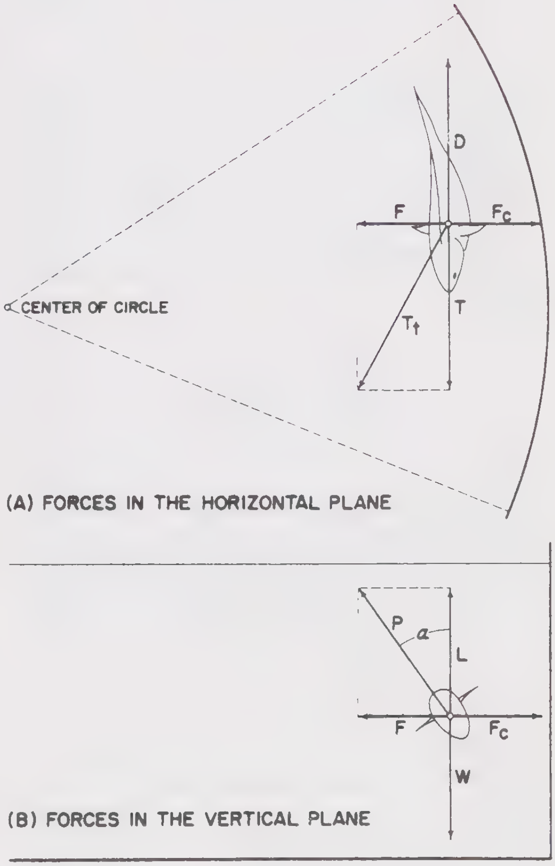
D
F
Fc
CENTER OF CIRCLE
T
Tt
(A) FORCES IN THE HORIZONTAL PLANE
P
a
L
F
Fc
W
(B) FORCES IN THE VERTICAL PLANE

FIGURE 1.—Schematic description of forces acting on a fish when swimming in a curved path. A. Forces in the horizontal plane. B. Forces in the vertical plane.

Analysis

For a neutrally buoyant fish swimming horizontally in a straight line at a constant speed the force balance in that plane (excluding forces due to buoyancy and its compensation) is, in absolute values,

$$T = D \tag{1}$$

where T is the thrust and D is the total hydrodynamic drag. Equation (1) also describes the force balance in the tangential direction for curvilinear motion. However, an additional balance must be made between the natural centrifugal force F_c driving the fish to stay in a straight line and the countering centripetal force F causing it to remain on a curved path (see Figure 1A). This force F, which is equal in magnitude and opposite in sign to F_c, is of magnitude

$$F = \frac{m^1 U^2}{R} = \frac{VU^2}{R}\,(\rho_f + \rho_w \lambda) \tag{2}$$

where m^1 is the virtual mass of the fish, ρ_f is the density (averaged) of the fish, V is its volume, U is the forward speed of the fish, λ is the longitudinal added mass coefficient, and R is the instantaneous radius of the curved path. The added mass coefficient λ is multiplied by the density of water ρ_w as the added mass is the volume of water dragged along with the fish. The hydrodynamic drag can be written as (Hoerner 1965)

$$D = \frac{1}{2}\rho_w V^{2/3} U^2 C_{Dt} \qquad (3)$$

where C_{Dt} is the total drag coefficient based on the two-thirds power of the volume, as reference area. Here drag includes gill drag, induced drag due to pectoral fin extension and lift, etc. (see Magnuson 1978 for an excellent description of the various components of drag).

To find the relative importance of the centripetal force, we divide Equation (2) by Equation (3), obtaining

$$\frac{F}{D} = 2\frac{V^{1/3}}{RC_{Dt}}\left(\frac{\rho_f}{\rho_w} + \lambda\right) \qquad (4)$$

showing that the fish's velocity does not influence the ratio of centrifugal to drag forces in this case. Equation (4) can now be used to obtain the correction to the force produced by the fish, since the total force T_t that the fish requires for swimming in a circular path in the horizontal plane is, by vectorial addition,

$$T_t = \sqrt{D^2 + F^2} \qquad (5)$$

Dividing by D^2 and applying Equation (1), we obtain the required thrust increase for neutrally buoyant fish, as a function of what will now be called the correction factor F/D,

$$\frac{T_t}{T} = \sqrt{1 + \left(\frac{F}{D}\right)^2}. \qquad (6)$$

Most studies of respiration and energetics in fish measure the aerobic oxygen consumption of the test animals as an indication of energy consumption. To obtain the correction required when the test data are obtained in a round tank, we recall that, for constant speed swimming

$$\dot{E} = TU \qquad (7)$$

where $\dot{E}$ is the rate of working. Thus the ratio of work (per unit time) for a continually turning fish, compared with that of fish swimming in a straight line at the same speed, is

$$\frac{\dot{E}_t}{\dot{E}} = \frac{T_t U}{TU} = \frac{T_t}{T}. \qquad (8)$$

The basic assumption of such respiration studies is that the oxygen uptake rate V_{O_2} is directly proportional to $\dot{E}$, so that

$$\frac{\dot{V}_{O_2 t}}{\dot{V}_{O_2 s}} = \frac{T_t}{T} \qquad (9)$$

and with Equation (4) we can write this ratio in terms of experimentally measurable quantities:

$$\frac{\dot{V}_{O_2 t}}{\dot{V}_{O_2 s}} = \sqrt{1 + 2\frac{V^{1/3}}{RC_{Dt}}\left(\frac{\rho_f}{\rho_w} + \lambda\right)^2} \qquad (10)$$

i.e., the equivalent oxygen uptake for a free-swimming fish moving in a straight line is always lower than that measured in a round tank. Also, for a given turning radius, the larger the fish, the greater the increase in oxygen uptake, or conversely, for a given fish, the oxygen uptake increases with decreasing turning radius. The increase is almost independent of swimming speed except for a possible weak Reynolds number dependence of C_{Dt}, neglected here.

The method shown above for obtaining the centripetal force by increasing the thrust is one possibility. A different way of getting the required forces is by means of hydrodynamic lift.

Negatively buoyant fish, such as most of the scombrids, produce lift by swimming continuously in order to maintain a horizontal course. This defines a hydrodynamical minimum swimming speed for horizontal motion (Magnuson 1970) and causes an additional effect due to swimming in a curved path.

The lift required is usually produced by the pectoral fins being placed at a small angle of incidence to the direction of motion. This force is at right angles to the longitudinal axis of the fish. It can therefore be applied to the production of the centrifugal force, by banking towards the center of curvature (see Figure 1B). Such behavior is an alternative to the added asymmetric thrust calculated above [Equations (4)-(6)], as no direct extra thrust is needed. However, the total lift force on the fins is now larger (Figure 1B), resulting in higher induced drag (Webb 1975; Magnuson 1978), which increases the thrust required.

For motion at a given speed we assume that the only component of drag that varies between straight-line and circular swimming is the induced drag. This is probably an underestimate, because the friction and form may also increase slightly, as mentioned in the previous section. Neglecting these, however, we find that the drag when turning D_t (the drag D, appearing in Equations (1)-(9), is D_t) is greater than the straight-line drag at the same speed D_s by

$$D_t - D_s = D_{it} - D_{is} \tag{11}$$

where D_{it} and D_{is} are the induced drag in turning and in straight-line swimming, respectively. The drag is usually (Hoerner 1965) written as a function of the fin lift force G

$$D_i = \frac{2G^2}{\epsilon \pi \rho b^2 U^2} \tag{12}$$

where b is the fin span and ϵ a fin shape factor. For our purposes, D_i can be written as

$$D_i = K \frac{G^2}{b^2 U^2} \tag{13}$$

as the quantities collected in K are invariant for a given fish.

The fin span is variable, as many species of interest can adjust the sweepback angle, changing the span.

Substituting Equation (13) in Equation (11) and applying the geometrical relations of Figure 1B

$$D_t - D_s = \frac{K_1}{U^2}\left(\frac{P^2}{b_t{}^2} - \frac{L^2}{b_s{}^2}\right), \tag{14}$$

where b_t and b_s are the pectoral fin span in turning and in straight-line swimming, respectively. Dividing by D_s,

$$\frac{D_t}{D_s} = 1 + \frac{K_1}{U^2 D_s}\left[\frac{P^2}{b_s{}^2}\left(\frac{b_s}{b_t}\right)^2 - \frac{L^2}{b_s{}^2}\right]. \tag{15}$$

However, $D_{is} = K_1 L^2 / U^2 b_s$, so that

$$\frac{D_t}{D_s} = 1 + \frac{D_{is}}{D_s}\left[\left(\frac{P}{L}\right)^2 \left(\frac{b_s}{b_t}\right)^2 - 1\right]$$

$$= 1 + \frac{D_{is}}{D_s}\left[\left(\left(\frac{F}{L}\right)^2 + 1\right)\left(\frac{b_s}{b_t}\right)^2 - 1\right]. \tag{16}$$

In horizontal swimming $L = W$, so that

$$\frac{D_t}{D_s} = \frac{\dot{V}_{O_2 t}}{\dot{V}_{O_2 s}}$$

$$= 1 + \frac{D_{is}}{D_s}\left[\left(\left(\frac{F}{W}\right)^2 + 1\right)\left(\frac{b_s}{b_t}\right)^2 - 1\right], \tag{17}$$

and as $W = (\rho_f - \rho_w)gV$, by substituting Equation (2)

$$\frac{V_{O_2 t}}{\dot{V}_{O_2 s}} = 1 + \frac{D_{is}}{D_s}\left[\left(\left(\frac{\rho_f + \lambda \rho_w}{\rho_f - \rho_w}\,\frac{U^2}{gR}\right)^2 + 1\right)\left(\frac{b_s}{b_t}\right)^2 - 1\right], \tag{18}$$

and again, as in Equation (10), the oxygen consumption is higher when the fish is swimming in a circular path. The two techniques, analyzed above are available to negatively buoyant fish, which can choose between producing the centripetal force by asymmetric thrust or by banking. Neutrally buoyant fish would have a more difficult time using the banking method [Equation (18)], as the vertical component L would cause upward motion, or complicated and strenuous compensatory motions.

Returning to the negatively buoyant species, such as skipjack tuna, *Katsuwonus pelamis*, it is reasonable to assume that they will choose the less costly method, or a combination of the two techniques. This will be studied quantitatively in the next section, but one can see immediately that the banking method is highly dependent on swimming speed. This indicates that there may be a threshold speed for each species above which the banking method is more costly.

Next, we estimate the influence of swimming in a curved path on the hydrodynamic minimum swimming speed (Magnuson 1970). At the minimum swimming speed, the pectorals are already producing the highest possible lift coefficient C_L (which will be designated as $C_{L\max}$). Banking the fins reduces the vertical component of the force (Figure 1B), since part of the hydrodynamic force is used to turn the fish. But the vertical force is prescribed by the weight, so that the swimming speed must be increased to obtain the required forces. Thus, the minimum swimming speed for moving in a curved path is always higher than that for swimming along a straight line. This further increases the effort required to swim in circular tanks above and beyond the thrust corrections found before, when the fish wants or has to move at minimum speed.

At the minimum speed U_m

$$W = \tfrac{1}{2} \rho_w A_f C_{L\,\max} U_m{}^2 \qquad (19)$$

where W is the submerged weight of the fish and A_f is the fin lifting area. If the fish turns (when it is confined to a round tank) and still remains at minimum speed, the pectoral fins are banked. The force produced on the fins is then (see Figure 1B)

$$P = \sqrt{W^2 + F^2} \qquad (20)$$

or

$$\frac{P}{W} = \sqrt{1 + \left(\frac{F}{W}\right)^2} \qquad (21)$$

P is produced while the fins are at $C_{L\max}$ so that

$$P = \tfrac{1}{2} \rho_w A_f C_{L\max} U_t{}^2 \qquad (22)$$

where U_t is the minimum speed for a horizontal turn. This is a function of the turning radius, through F [see Equation (2)].

Substituting Equations (22), (19), and (2) in Equation (21) we have

$$\left(\frac{U_t}{U_m}\right)^2 = \sqrt{1 + \frac{m^1 U_t{}^2}{RW}} \qquad (23)$$

$$\left(\frac{U_t}{U_m}\right)^4 = 1 + \frac{2m(1 + \lambda \rho_w/\rho_f)}{\rho_w R A_f C_{L\max}} \left(\frac{U_t}{U_m}\right)^2 \qquad (24)$$

from which

$$\frac{U_t}{U_m} = \left[B\left(1 + \sqrt{1 + \frac{1}{B^2}}\right)\right]^{1/2} \qquad (25)$$

where $B = \dfrac{m\left(1 + \lambda \rho_w/\rho_f\right)}{\rho_w C_{L\max} A_f} \; \dfrac{1}{R}$.

From Equation (25) we see that $U_t > U_m$ for all finite values of R and that the minimum swimming speed grows as the radius decreases. The increase in minimum speed also is reflected in the total effort required for swimming in the round tank, as the rate of working goes up as the cube of the velocity. The induced drag changes [Equation (11)] are included since the fins are producing maximum lift coefficients both in straight-line swimming and in turning

$$\left(\frac{\dot V_{O_2 t}}{\dot V_{O_2 s}}\right)_{\text{minimum speed}} = \left(\frac{U_t}{U_m}\right)^3 . \qquad (26)$$

Results and Discussion

To estimate the actual significance of the various corrections developed in the previous section, numerical values of the parameters are now substituted for a negatively buoyant species, the skipjack tuna.

Most of the quantities appearing in the oxygen consumption ratios [Equations (10), (18), and (26)] are easily measurable. The added mass and drag coefficients (λ and C_{Dt}) are more difficult to obtain, as both may also be dependent on the turning radius (due to higher drag when turning and additional added mass effects due to the fish body curvature). However, no such information is presently available, so both these quantities have to be estimated from data on rigid engineering structures.

The most complete set of data for estimation of D appears in Magnuson (1978, table 6) for skipjack tuna. These data will now be used to obtain a typical value of the correction factor Equation (4). The total drag for a 44 cm skipjack tuna swimming at 66 cm/s was estimated to be 19,780 dyn. The mass of the fish is approximately 1.67 kg (Nakamura and Uchiyama 1966), and with an average density of 1.09 (Magnuson 1978, table 3) the volume of the fish is 1,530 cm^3. The drag coefficient C_{Dt} (which is different from Magnuson's drag coefficient because of the different reference area) is found, from Equation (3), to be

$$C_{D\,t} \simeq \frac{2 \cdot 19{,}780}{1.025 \cdot (1{,}530)^{2/3} \cdot 66^2} \simeq 0.067 . \qquad (27)$$

Magnuson's (1978) data are partially based on the study of ram ventilation by Brown and Muir (1970) which was carried out in the holding tanks of the National Marine Fisheries Service Kewalo Research Facility in Honolulu, which are of 7.3 m in diameter. These allow a maximum path radius of about 300 cm. Recalling that the longitudinal added mass for a streamlined fish shape is $\lambda \approx 0.2$ (Webb 1975) and substituting the above values first into Equation (4), we obtain

$$\frac{F}{D} = 2\,\frac{(1{,}530)^{1/3}\ (1.06 + 0.2)}{300 \cdot 0.067} = 1.44\,. \quad (28)$$

This means that the centripetal force is actually larger than the total drag force under these circumstances. The total force exerted by the fish swimming in a circular path of 300 cm radius is thus, from Equation (6), $T_t/T = 1.76$, i.e., 76% greater than that required for straight swimming at the same speed. This is also, from Equation (9), the ratio of oxygen consumption. The ratio F/D grows essentially proportionally to fish length, so that larger fish expend an even greater proportion of energy in swimming in a curvilinear path.

We now look at the ratio of oxygen consumption obtained for fish swimming under the same circumstances while banking their fins. This is calculated from Equation (18), assuming that at this low (close to minimum) speed the pectoral fins are fully stretched so that $b_s/b_t = 1$. The ratio D_{is}/D_s is found from Magnuson's (1978) table 6, to be approximately 0.3;

$$\frac{D_t}{D_s} = \frac{\dot{V}_{O_2t}}{\dot{V}_{O_2s}} = 1 + 0.3\left[\left(\left(\frac{1.09 + 0.2 \cdot 1.025}{1.09 - 1.025}\ \frac{66^2}{981 \cdot 300}\right)^2 + 1\right) \cdot (1) - 1\right] = 1.026\,, \quad (29)$$

i.e., the increase in energy requirements is only 2.6%, much less than for the asymmetric thrust, nonbanked type of swimming. We can conclude therefore that skipjack tuna moving at low speeds in circular paths will use the banked swimming technique once they are adjusted. The banking angle can be obtained by banking the body and keeping symmetrical fin angles (as in Figure 1B), or by asymmetric deployment of the pectorals. An experimental program to study these angles by photography is underway at present, as this is the most obvious and easily measured prediction of the present theory. The predicted value of the banking angle (from the vertical) is obtained from Equation (20) as

$$\tan\alpha = \frac{F}{W} \qquad \alpha = \tan^{-1}\frac{m\left(1 + \dfrac{\lambda\rho_w}{\rho_f}\right)U^2}{RW}\,, \quad (30)$$

which for the skipjack tuna example above is 12.0°.

We see above that the banking technique is much more efficient at a relatively low swimming speed. However, the ratio of energy consumption [Equation (18)] is proportional to the speed to the fourth power, so it is important to check on its values at higher swimming speeds. There is no complete set of data available for such speeds, so we have to make some assumptions about the behavior of the various parameters. The ratio D_{is}/D_s is most probably not speed-dependent, as the total and induced drag are both proportional to the speed squared. Thus, we can use the value 0.3 found above. Next, we assume that fin extension is the same (at each speed) for straight-line swimming and turning (the extension can change as a function of speed, but the ratio remains constant). This assumption will also be checked in the experimental program mentioned before, as it is easily corrected in Equation (18).

Skipjack tuna can move at up to 10 body lengths/s, i.e., over 400 cm/s in the present case. Applying Equation (18) at different speeds (still for a turning radius of 300 cm), we obtain

U cm/s	66	100	120	150	175	200	300	400
$\frac{\dot{V}_{O_2t}}{\dot{V}_{O_2s}}$	1.026	1.137	1.285	1.696	2.289	3.199	12.13	36.18

i.e., at speeds of about 160 cm/s (≈ 4 body lengths/s) the asymmetric thrust method, which is independent of speed, becomes the better way of compensating for circular swimming. One can therefore establish a general upper limit for the centrifugal increase in oxygen consumption from Equation (10), with the proviso that at lower speeds the banking method is more efficient.

Next, we calculate the increase in the minimum swimming speed of the tuna mentioned above, for which $m = 1{,}670$ g, $C_{L\max} = 1.0$, $A_f = 36$ cm^2 (Magnuson 1973), $\rho_w = 1.025$, $\lambda = 0.2$, and $R = 300$ cm. From Equation (25) we obtain $U_t/U_m = 1.093$. The measured minimum speed in the round tank is thus 10% higher than for the same fish moving in a straight line.

Using the allometric data of Magnuson (1973), we can obtain U_t/U_m as a function of fish size for various species. This appears in Figure 2 for the

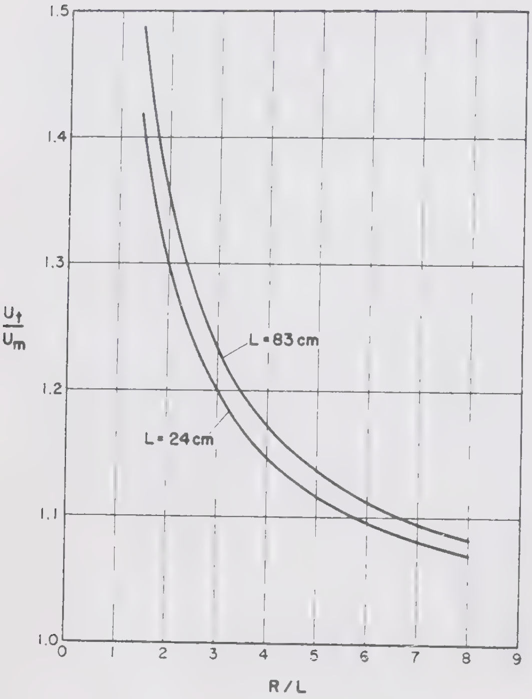

FIGURE 2.—Ratio of minimum speed when moving in a circular path, to the minimum speed in straight-line swimming versus the ratio of turning radius to fish length, for skipjack tuna, *Katsuwonus pelamis*.

skipjack tuna, for which $m = 0.00490L^{3.36}$ and $A_f = 0.00749L^{2.24}$, so that a slight dependence on fish length is retained, even after normalizing by the length. These curves can now be used to establish the increase in minimum energy consumption, with the aid of Equation (26).

In conclusion, it is seen that running fish in circular tanks can cause very significant additional stresses. These have to be taken into account when applying data collected under such circumstances to naturally occurring situations.

Acknowledgments

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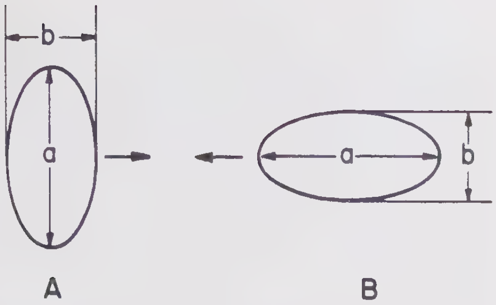

Fig. 2. Motion of an elliptical cylinder of 2:1 aspect ratio normal to (2A) and parallel to its large axis (2B).

of the body is moved sideways with an amplitude increasing to a peak at the caudal peduncle, as part of the anguilliform swimming mode. The larger amplitudes here are needed to drive the caudal fin which in turn provides a large part of the thrust required for swimming. These lateral excursions can therefore not be eliminated but their energetic cost can be reduced to increase efficiency. Again, this is achieved by producing a roughly elliptical section which moves in the direction of its large axis. To further decrease the drag on the peduncle region, some species have developed long appendages on the second dorsal and ventral fins (Fig. 1), or even series of finlets which serve as flow vanes, decreasing the shedding of vorticity and drag (Aleyev, 1977). The horizontal flattening of the peduncle has an additional function (Magnuson, 1970) producing a part of the lift required to counteract negative buoyancy in some species. Finally, the caudal fin is elongated vertically to produce a large, high aspect-ratio hydrofoil propelling the fish by sideways motions. Another adaptation advantageous to rapid maneuvering is the "double tail" produced by the second dorsal and ventral fins, in front of the caudal fin.

In conclusion, the observed changes in body section shape, as a function of distance from the head, help reduce the effort required for maneuvering and cruising. This improvement is in addition to the lateral instability mentioned by Thomson and Simanek (1977) as aiding maneuverability. An increase in mouth ingestion area, and improved stereoscopic vision may well be additional beneficial results of this adaptation.

Acknowledgments.—This note was written while I was NRC-NOAA Senior Research Associate at the NOAA Southwest Fisheries Center, La Jolla. I would like to thank J. R. Hunter and R. Lasker for their hospitality and Ken Raymond for assistance with the graphics.

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VOLUNTARY SWIMMING SPEEDS OF TWO SPECIES OF LARGE CARCHARHINID SHARKS.—The elasmobranchs (sharks, skates and rays) have survived virtually unchanged for hundreds of millions of years, indicating an extremely successful adaptation. Very little information exists, however, on the behavior (Gruber and Myrberg, 1977) of the larger sharks, mainly because of the difficulties of observing these fish in the ocean (Nelson, 1977) and of keeping them under controlled conditions that simulate their life in the wild.

Most pelagic sharks are negatively buoyant (Budker, 1971) and must, for this reason, move continuously to counter their tendency to sink. This motion, which is also applied to seeking

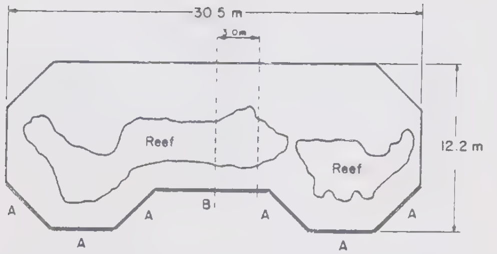

Fig. 1. Schematic description of aquarium. A indicates the smaller and B the larger viewing windows. The reef at all points is at least 3.0 m deep.

prey and oxygenating the gills, is a major fraction of the shark's energy budget. To understand and predict shark behavior, the swimming speed has to be known. In this note the voluntary swimming speeds of two species of sharks (*Carcharhinus leucas* and *Carcharhinus plumbeus*) are measured and compared to theoretical predictions based on energetical considerations (Weihs, 1977).

Observations on the swimming speed of bull (*C. leucas*) and sandbar sharks (*C. plumbeus*) were conducted in a 1.5 million liter enclosed aquarium, 30.5 m long, 12.2 m wide, and 4.7 meters deep at the deepest point. Six 2.4 m × 3.7 m and one 2.4 m × 7.3 m acrylic viewing panels allowed underwater observation. The pool is of elongated shape with a natural appearing concrete "rocky" reef occupying approximately 25% of the floor (Keyes, 1979) (Fig. 1). Viewing from the top was possible from all sides.

The tank contained two *C. leucas* (2.0 and 2.3 m total length [TL]) in addition to five *Negaprion brevirostris* (≃2 to 3 m TL), two *Negaprion acutidens* (≃1.5 to 2.0 m TL), four *C. plumbeus* (≃2 to 2.5 m TL) and seven *Ginglymostoma cirratum* (≃1.5 to 3.0 m TL). A population of the cleaner wrasse *Labroides dimidiatus* occupied the reef and functioned in removing parasites from the sharks. Total length of the sharks (the distance from the anterior margin of the snout to the most posterior point of the caudal fin) was converted to standard length (SL) following Bass et al. (1973).

A 3 m wide section of the rectangular part of the aquarium (Fig. 1) was marked by lines 6 mm wide, 0.5 m above the water surface so as not to interfere with the sharks' swimming. The 3 m section was chosen so the measurement error due to observer delays would be less than 5%, longer straight sections not being possible because of effects of the round parts of the tank. The swimming speed was obtained by measuring the time elapsed between the snout passing beneath the two marker strips. Only events including straight-line swimming perpendicular to the markers were recorded. Preliminary observations indicated that disturbances such as cleaning the tank, external construction noises, and encounters with other sharks during or just before the event, caused changes in their behavior. Measurements were carried out during both day and night (the difference being in lighting level, 4,000 W direct lighting during daytime and dim indirect lighting at night, as well as the absence of spectators at night). There was no significant difference between day and night swimming speed averages (the difference was less than ½ the standard error). The aquarium temperature was maintained at 26 ± 1 C. The sharks were fed in the early afternoon on mondays, wednesdays and fridays. The only differences noted were just prior to, during and immediately after feeding. Only data collected more than 3 hours before and 6 hours after feeding were therefore used for the volitional speed analysis.

The sharks were observed to have preferred swimming patterns when undisturbed, making it easier to define "valid" measurements. These patterns, and their social significance, are being studied separately and will be described in due course. Social hierarchy was indicated, where individuals lower on the social order maneuvered to keep out of the more dominant individuals' trajectories. As a result of this "social behavior," only two individuals were seen to have undisturbed motion. These were Bull No. 2 (2.3 m TL) and Sandbar No. 1S (≃2.1 m TL). Bull No. 1 (2.0 m TL) also exhibited regular motion, but was somewhat influenced by the presence of Bull No. 2. Measurements of the speed of these three individuals were included in the final analysis.

Following preliminary observations on all individuals of the pelagic species available in the aquarium, 209 swimming sequences of Bull No. 2 were timed to examine uniformity, effects of outside disturbances, encounters and proximity to feeding time. Disturbed sequences, events where turning or non-level swimming occurred, and times measured close to feeding were deleted, leaving 88 measurements (Table 1). These results show the very narrow spread of speeds for Bull No. 2 and Sandbar No. 1S

Table 1. Voluntary Swimming Speeds of the Experimental Sharks.

Individual	Number of measurements	Average speed cm/sec	Standard error cm/sec	Highest measurement cm/sec	Lowest measurement cm/sec
C. leucas No. 2	88	62	±4	70	56
C. leucas No. 1	13	72	±6	83	68
C. plumbeus No. 1S	18	64	±2	67	60

nd the somewhat elevated speed and greater ariability of measurements of Bull No. 1. The atter may be a result of the presumed lower osition of Bull No. 1 in the social hierarchy in elation to Bull No. 2.

Fig. 2 shows the average volitional speeds of he three sharks (including the standard error) s a function of their standard length (L). The full line on Fig. 2 is the theoretical prediction of the volitional swimming speeds as a function of standard length (Weihs, 1977). This prediction is based upon an energetic cost optimization. The hypothesis is that an undisturbed fish will swim at a speed at which it requires minimum energy per unit distance traversed, which occurs when the total metabolic rate is approximately double the standard rate. This predictive approach has proved successful for various freshwater and seawater species (Weihs, 1975; Gooding and Neill, 1980) such as trout and tuna and is shown here to describe elasmobranch behavior also. Some further evidence of an elasmobranch conforming to this behavior can be obtained from a recent study of *Squalus acanthias* by Brett and Blackburn (1978). They show the routine metabolism of the dogfish to be approximately twice that of the resting standard metabolism, which corresponds to the predicted ratio (Weihs, 1977). The observed swimming was irregular because of geometric limitations of the respirometer so that voluntary speeds were not obtained.

The theoretical prediction of voluntary swimming speeds of approximately 68 cm/sec for sharks at 2 m SL has been verified for *C. leucas* and *C. plumbeus*. Other species available at the Sea World San Diego aquarium, as well as other individuals of *C. plumbeus*, could not be examined quantitatively because of greater variability in their behavioral patterns. The speeds, when measured, however, also were close to the predicted values (60–75 cm/sec).

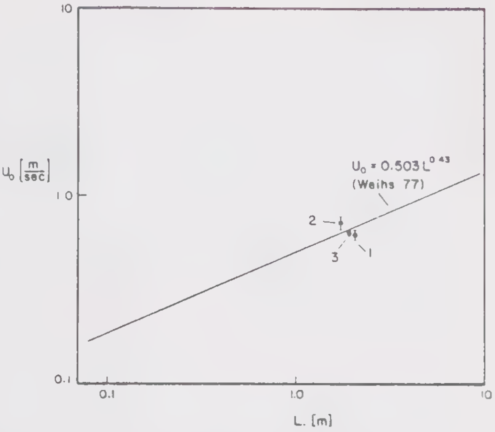

Fig. 2. Voluntary swimming speed, U_0, versus standard length (L) of three individual sharks. (1) *C. leucas* No. 2, (2) *C. leucas* No. 1, (3) *C. plumbeus* (average and standard error of experimental data). Full line indicates theoretical prediction.

The close agreement between theory and experimental measurements at the Sea World facility indicates that these data will be typical of field results. These measurements also give further encouragement to the possibility of predicting behavioral patterns of these largely unknown and highly interesting animals by theoretical means.

Acknowledgments.—This work was done while the senior author was visiting the NOAA/NMFS Southwest Fisheries Center, La Jolla, as a NRC Senior Research Associate. We would like to thank R. Lasker and J. R. Hunter for critically reading the manuscript.

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FORMULAE VARIATIONS OF PHARYNGEAL TOOTH COUNTS IN THE CYPRINID GENUS *NOTROPIS*.—Identification of fishes in the Cyprinidae and Catostomidae is often based in part on the number and arrangement of pharyngeal teeth that occur on the fifth pair of ceratobranchials (Moore, 1988). However, few studies have been undertaken to examine the intraspecific variation that may occur in these counts which could lead to misidentification.

Variation in a number of fundamental characters in the genus *Notropis* was examined by Fowler (1910). Other studies on cyprinids are reviewed by Eastman and Underhill (1973); most species reported on have less than 20% variation from the expected count. Of the 42 additional cyprinid species examined by Eastman and Underhill (1973), only two deviated from the expected count more than 10% of the time.

Materials and methods.—Pharyngeal tooth counts from 100 individuals of the following eight species of the genus *Notropis* were examined: *N. albeolus*, Jordan, *N. analostanus* (Girard), *N. boops* Gilbert, *N. greenei* Hubbs and Ortenburger, *N. photogenis* (Cope), *N. scabriceps* (Cope), *N. whipplei* (Girard) and *N. zonatus* (Putnam). Specimens were provided from the museum collection of the Appalachian Environmental Laboratory. When possible, specimens of each species examined were taken from the same collection to limit any deviations that could be attributed to geographic variation. Satinfin shiners (*N. analostanus*) were analyzed from collections within the same drainage taken during a 3-day period in 1976.

Arches were removed, carefully cleaned and inspected with the aid of watchmaker's forceps, an insect pin and a dissecting microscope. Counts (Hubbs and Lagler, 1964) for each individual fish were recorded in order to examine asymmetrical variability in formulae. Empty sockets were counted, however, care was taken not to count tooth crowns embedded within the mucosa of the arch that were destined to replace teeth already present. Any fish in which either arch broke along the tooth forming area upon removal was eliminated from the results.

Results and discussion.—Expected pharyngeal tooth formulae and observed counts for each species are presented in Table 1. All fish exhibited a most common tooth count with various numbers of deviant formulae. *N. photogenis*, with a most common formula of 2,4-4,2, had the most invariable count with only 3% of those examined possessing a different count. A mean deviation of 12.5% existed among the five species examined having this count. The remaining species (Table 1) most often possessed a 1,4-4,1 count with a mean deviation of 25%. *N. boops* was found to have counts varying from its usual 1,4-4,1 formula 36% of the time. The most consistent counts in this study were among fishes possessing the 2,4-4,2 expected formula.

Eastman and Underhill (1973) found a few instances of additions to the secondary row, but we did not. Additions and deletions to the primary row also occurred, the former occurring more frequently than the latter (Table 1). Eastman and Underhill (1973) suggested that additions improve the masticatory process and may be selected for. However, the limited number found in this study is probably more likely due to faulty tooth replacement (Evans and Deubler, 1955; Weisel, 1967), rather than an evolutionary trend.

Hubbs and Hubbs (1944) reported that variant asymmetrical tooth counts in western North American minnows tended to favor the left arch. Eastman and Underhill (1973) also noted this in tooth formulae in Minnesota cyprinids.

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AN ECOLOGICAL PERSPECTIVE OF THE EFFECTS OF MONOCYCLIC AROMATIC HYDROCARBONS ON FISHES

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INTRODUCTION

Monocyclic aromatic hydrocarbons (MAH) constitute a major class of petrochemicals potentially affecting organisms in the aquatic environment, but they have not received much attention in pollution research. MAH are highly toxic and relatively water-soluble when compared with other classes of petroleum hydrocarbons. However, the assumption has been made for some time that they are so volatile they do not persist in the aquatic environment long enough to affect organisms. We think this assumption is unfounded, based upon inadequate field measurements, and arises from considering these compounds only in relation to oil spills when a single large input occurs. The potential chronic sources of these compounds and their effects on aquatic organisms, particularly in estuaries, have been largely ignored. In addition, most studies of monocyclic aromatics have been conducted in laboratories, testing the effects of high lethal and sublethal levels. The actual occurrence of these compounds in water and organisms in the field, and their potential effects at low chronic levels in relation to other environmental factors, are still relatively unknown.

This paper attempts to: 1) summarize present knowledge of the effects of monocyclic aromatics on fishes, 2) provide an ecological perspective of the effects of these compounds on

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fishes, 3) hypothesize modes of action of monocyclic aromatics on fishes and, finally, 4) suggest directions of research needed to determine whether these compounds may represent a threat to our fisheries resources.

Most laboratory studies of the effects of monocyclic aromatics on fishes have been done at the National Marine Fisheries Service laboratories at Tiburon, California, Auke Bay, Alaska and Seattle, Washington and these studies are emphasized in the following discussion. The authors' experience with monocyclic aromatic compounds centers around our laboratory and field studies on fishes of the San Francisco Bay area. We realize that other ecosystems will differ on many points.

Measurements and observations made in our experiments have led us to hypothesize some modes of action of monocyclic aromatics on fishes. The discussion on their effects is placed in the context of these hypotheses. When studies substantiating our hypotheses are available, references are provided. It should be realized, however, that this synthesis is offered primarily to provide a research framework and does not necessarily imply that the hypotheses have been completely validated.

DEFINITION, PROBABLE SOURCES AND FATES OF MONOCYCLIC AROMATIC HYDROCARBONS

We do not intend to provide a comprehensive discussion of the chemistry of the monocyclic aromatic hydrocarbons (MAH), but for the benefit of the reader unfamiliar with these compounds, the following summary of their characteristics, sources and probable fates is provided.

Structure and Chemical Characteristics

Aromatic hydrocarbons are designated aromatic primarily because the earliest known representatives were distinguished by marked aromatic odors. Monocyclic aromatics are substances containing one benzene ring. The benzene ring is characterized by a cyclic arrangement of carbon and hydrogen atoms with a resonant bonding structure: an unsaturated, symmetrical ring of six equavalent CH groups (Gerarde, 1960). The simplest monocyclic compound is benzene itself, consisting of one ring, with no substitutions (Fig. 1). Other common MAH include toluene (one substituted methyl group), ethylbenzene (one substituted ethyl group) and the isomers of

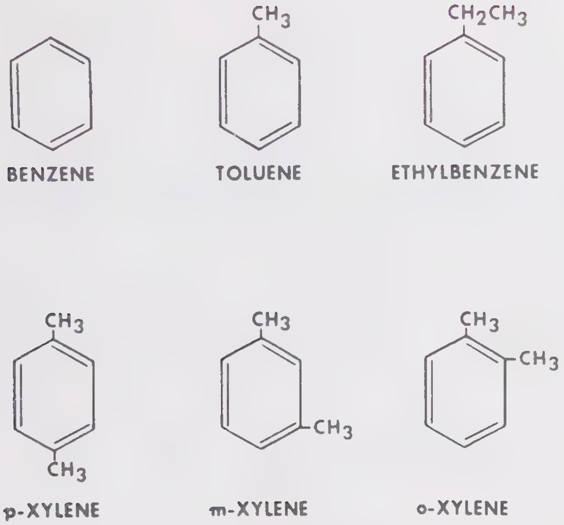

FIGURE 1. Six common monocyclic aromatic hydrocarbons. Unsymmetrical formulas (Kekulé) are used to represent the symmetrical molecules for simplicity.

xylene: *p*-xylene, *m*-xylene and *o*-xylene (three isomeric arrangements of two methyl groups). Some physical and chemical characteristics of these six monocyclics are summarized in Table 1. There are many other possible substituents on the benzene ring; these compounds will be referred to here, for purposes of simplification, as substituted benzenes.

MAH, for example benzene, are relatively soluble in water (Table 1) when compared with other petrochemicals. Since most research on the effects of MAH on fishes has been done with benzene and toluene, these particular compounds are most often discussed in this paper.

Potential Sources

Aromatic hydrocarbons have been used in industry for some time and benzene, toluene and xylene are three of the most important organic chemicals in industry. Recent data on the production of benzene, for example, showed an exponential increase in production in the last twenty years from less than 0.5 billion gallons in 1960 to about 1.5 billion gallons in 1979 (Davis and Magee, 1979).

The aromatic hydrocarbons obtained from petroleum and their derivatives come under the definition of petrochemicals-

TABLE 1. Physical - chemical properties of six prevalent monocyclic aromatic hydrocarbons. Data synthesized from Gerarde (1960) except where otherwise indicated.

Component	Molecular weight	Boiling point (°C) (760 mm Hg)	Melting point (°C)	Vapor pressure (mm Hg)	Index of refraction	Solubilities	
						FW[a] 0 ppt (ppm)	SW[b] 25 ppt (ppm)
Benzene	78.11	80.1	+ 5.5	74.6 (20 C)	1.502 (20 C)	2026	1400
Toluene	92.13	110.6	-94.5	36.7 (30 C)	1.489 (24 C)	595	330
Ethyl-benzene	106.16	136.2	-94.9	10.0 (25.9 C)	1.493 (20 C)	175	180
para-Xylene	106.16	138.3	-55.9	10.0 (27.3 C)	1.500 (21 C)		180
meta-Xylene	106.16	139.1	-54.2	10.0 (28.3 C)	1.497 (20 C)		210
ortho-Xylene	106.16	144.4	-13.3	10.0 (32.1 C)	1.506 (20 C)	195	230

[a] Fresh water - McAuliffe, 1966. 25°C and 0 ppt. Converted data to ml/liter.

[b] Sea water (estuarine) - Benville and Korn, 1977. 16°C and 25 ppt.

chemicals derived from petroleum or natural gas. The primary sources of MAH in the aquatic environment are from industrial petrochemicals and from crude oil. Some principal uses of MAH in industry are as: 1) starting materials and intermediates for synthesis of plastics, paints, pesticides, protective coatings, resins, dyes, drugs, flavors, perfumes, vitamins, explosives; 2) solvents for paints, dyes, resins, inks, lacquers, rubber, plastics and pesticides; and 3) constituents of aviation and automotive gasoline.

The MAH may also comprise from about 20 to 50% of the water-soluble fraction (WSF) of crude oil, depending upon the type of crude oil (Anderson *et al.*, 1974b; Clark and MacLeod, 1977). Some crude oils are more aromatic and toxic in that they contain higher proportions of aromatics including monocyclics.

More specifically, we believe a major source of MAH petrochemicals in the San Francisco Bay estuary is from their use in pesticide mixtures as synergists, inhibitors, solvents, emulsifiers, wetting agents, etc. (Wiens, 1977). Petroleum products are also applied directly for control of insects, mites, weeds and fungus. A computer summary of the top 50 pesticides in terms of total pounds (extracted from the 1978 pesticide use reports for California)(State of California, 1978; Jung and Bowes, 1980) shows that aromatic petroleum hydrocarbons are heavily used in the ten counties forming the watershed draining into the San Francisco Bay-Delta. Six of the top ten chemicals listed include categories such as "petroleum hydrocarbons, petroleum oil, petroleum distillates, xylene, aromatic petroleum solvents, xylene-range aromatic solvents and petroleum distilled aromatics", totaling about 5 million pounds applied to 1.3 million acres.

There are other major sources of petrochemicals in the San Francisco Bay-Delta area, including municipal and industrial discharges, particularly in the Carquinez Straits area, which is along a major fish migratory pathway and also an area where fish kills consistently occur in summer (Kohlhorst, 1973). In fact, municipal effluents are probably among the major sources of petroleum input to the Bay, discharging a total of at least 72,400 pounds per day of "oil and grease" (Risebrough *et al.*, 1978). Industrial discharges by refineries are apparently less-a total of 3,510 pounds per day (Risebrough *et al.*, 1978). The total oil and grease measurement does not include, however, a large proportion of the more toxic water-soluble fraction such as the aromatic hydrocarbon components and, thus, inadequately estimates the relative toxicity of the discharges (Wolfe *et al.*, 1979). Data from an API report (American Petroleum Institute, 1978) indicate that total MAH measured in refinery effluents can range from only traces up to approximately 100 ppb. Data also indicate the concentration in intake water is sometimes higher than in the effluents. The latter fact suggests that there may be chronic water levels of MAH in the 100 ppb range. The refineries listed in this report, however, are not identified, and some San Francisco Bay refineries may have lower or higher effluent concentrations. In addition to refineries, there are many other industrial dischargers of petrochemicals. We need to examine the amounts and effects of discharges more carefully, and further measurements of toxic components in receiving waters are needed, not only in San Francisco Bay, but also in other estuaries.

Other sources of MAH in San Francisco Bay include the increasingly frequent spills associated with oil transport and transfer activities. Petroleum refineries in the Bay currently account for 3 to 4% of the total volume of crude oil transported yearly by tankers throughout the world. The refineries in the northern area of the Bay process on the order of a million barrels of crude oil daily (approximately 136 thousand tons) and the total volume processed yearly is about 50 million tons (Risebrough *et al.*, 1978).

A minor source of MAH is from recreational boating activity, with input of many toxic aromatics through outboard motor gasoline effluent. At times this activity is considerable (Hirsch *et al.*, ms in prep. (a)).

The relative contribution of various sources to the concentration of MAH in the receiving waters of San Francisco Bay has not yet been quantified, but a study has been initiated with the cooperation of the State of California Water Resources Control Board (Jung and Bowes, 1980; Whipple, 1979, 1980). Concentrations of individual MAH from other areas are given below.

Fate of Monocyclic Aromatics in the Aquatic Environment

Little is known about 1) the partitioning of MAH into various compartments of an aquatic ecosystem, 2) the rates of exchange among these compartments, or 3) the relative importance of various pathways. The entire subject needs further study for this class of compounds and will not be discussed in detail here.

Table 2 summarizes some separate studies on various fates of MAH in aquatic systems. There appears to be no study attempting to bring these pathways into a single model for this group of compounds. A comprehensive discussion of the fate of petroleum hydrocarbons, in general, is given in a review by Clark and MacLeod (1977) and in papers by Butler *et al.*, (1976), Gordon *et al.*, (1976) and Karrick (1977).

TABLE 2. Major pathways for the fate of monocyclic aromatics (MAH) in the aquatic environment. Rates probably vary with several environmental factors, including wind and wave action, temperature, and salinity.

Pathway	General conclusions	Selected references
Dissolution	Relatively soluble--152-1780 ppm in fresh water; 180-1400 ppm in seawater (Table 1).	Benville and Korn, 1977 Burwood and Speers, 1974 McAuliffe, 1966, 1977a Wasik and Brown, 1973
Evaporation	Rapid—from single spill a few hours to 10 days.	Gordon _et al._, 1976 Harrison _et al._, 1975 McAuliffe, 1977b
Atmospheric Input	Probably considerable.	Wiens, 1977
Concentration at Thermocline	Indication from vertical sampling profiles that volatile aromatics are at higher levels at the position of the thermocline.	Myers and Gunnerson, 1976
Emulsification Colloidal Dispersion	Little known.	Davis and Gibbs, 1975 McAuliffe, 1977a
Agglomeration Sorption Sinking Sedimentation	Monocyclics, including benzene, probably sorb to particulate matter; sorption of benzene to particulate matter in seawater was 4.8-28.4 μg/mg of particulates.	Zsolnay, 1972, 1977
Microbial Modification	In laboratory studies, monocyclics are biodegraded; including benzene, toluene, xylenes, tri- and tetramethylbenzenes, alkylbenzenes, cycloalkyl benzenes. In the marine environment microbial degradation may be slower.	Gibson and Gibson _et al._, 1968 to 1977 (11 papers) Lee and Ryan, 1976 Marr and Stone, 1961
Photochemical Modification	There is preferential decomposition of aromatics.	Burwood and Speers, 1974 Hansen, 1977
Biological Ingestion and Excretion	Monocyclics are rapidly bioaccumulated from water to relatively high levels in adult fish and usually depurated rapidly. (Larval fish do not readily depurate, with high bioaccumulation resulting). Monocyclics are probably not bioaccumulated from food by fish.	See next few sections for references.

As previously discussed, MAH when compared to other petroleum hydrocarbons are relatively soluble in water. They also have high boiling points and vapor pressures (Table 1) and would be expected to volatilize from water relatively rapidly. This pathway has been assumed to predominate, with aromatics volatilizing too rapidly to affect aquatic biota. Monocyclics also undergo photooxidation and microbial modification. However, there is some evidence that MAH, e.g., benzene, are sorbed to sediments and possibly to organic aggregates. They may also be concentrated at thermoclines and haloclines. Reversing loss through evaporation, MAH may return to the water through atmospheric input. Finally, and most significantly, MAH do occur in the water and are taken up by aquatic organisms, including fish. The latter aspect of the fate of monocyclic aromatics is emphasized in this paper and discussed more fully below.

CONCENTRATIONS OF MONOCYCLIC AROMATICS IN WATER AND TISSUES OF FISH SAMPLED IN THE FIELD

In lakes, rivers and estuaries, such as San Francisco Bay, with continuous input of pollutants, there is some evidence that MAH, including benzene, are present (e.g., Brown *et al.*, 1979; Whipple, 1979) in both water and fish tissues. Table 3 summarizes some measurements of MAH in water samples taken from the field. As can be seen from these data, few measurements of individual monocyclic compounds have actually been made. Many measurements of aromatic hydrocarbons found in the literature, usually designated "total aromatics", do not include benzene and toluene, and usually, by most analytical methods, exclude ethylbenzene and xylenes.

One reason for the paucity of data on MAH may be the assumption that they are not present in sufficient concentration to be harmful. Another reason is that the measurement of these components requires special analytical techniques which have only recently become feasible for low concentrations. Most previous field measurements of petroleum hydrocarbons have been made of the alkane groups ($>C_7$) and a few aromatics with higher boiling points (polycyclic aromatic hydrocarbons, or PAH; Neff, 1979). The lower boiling point MAH are lost in the concentration step used in the analysis for polycyclic aromatics.

Table 3 includes only data where some estimate or measurement of the MAH is actually made. The range in open ocean waters appears to be from approximately 0.01 to 5 ppb. Closer to shore and in estuaries the range appears to be from

TABLE 3. Concentrations of monocyclic aromatics measured in the water column. Few data are available at the present time.

Location	Water Depth (meters)	No. of Samples	Hydrocarbon type	Hydrocarbon concentration (ppb)	References
Atlantic Ocean					
Skidaway River, GA	Surface	?	Benzene, toluene	3	Lee and Ryan, 1976
Tanker Route New York to Gulf of Mexico	Surface to 10	?	Total volatiles[a]	Med=0.1-0.3 Range=0.08-2.4	Myers and Gunnerson, 1976
Pacific Ocean					
San Francisco Bay	2	8	Total aromatics	$\leq$5-59	DiSalvo and Guard, 1975
San Francisco Bay	Surface	5	Total 6 aromatics[b]	1-50	Benville (unpublished)
Tanker route San Francisco to Cook Inlet	0-10	?	Total volatiles	Med=0.1-0.3 Range=0.01-4.0	Myers and Gunnerson, 1976
GEOSECS Tanker routes	0-10	223	Total volatiles	Mean=0.22 Range=0.01-4.32	Brown and Huffman, 1976
Offshore oil seep Coal Oil Point, CA	Surface	10	Benzene Toluene	ND-50 ND-80	Koons and Brandon, 1975
Baltic Sea and approaches					
Open water	1-200	6	Saturateds and monoaromatics	48-64	Zsolnay, 1972
Open water	1-200	40	Saturateds and monoaromatics	0-50	Zsolnay, 1977
Refineries[c]					
Refinery intake water	--	40	Benzene Toluene Ethylbenzene Total	Trace-40 Trace-15 Trace-20 Trace-65+	American Petroleum Institute, 1978
Refinery effluents	--	36	Benzene Toluene Ethylbenzene Total	Trace-30 Trace-60 Trace-40 Trace-90+	American Petroleum Institute, 1978
Fresh water lakes and rivers					
Fox River, Illinois (Industrial river)	?	?	Benzene Toluene	100-200 100	Brown *et al.*, 1979
Lake Chetek (Resort lake)	?	?	Benzene Toluene	8-9 90-100	Brown *et al.*, 1979
Lake of the Woods, Canada (Pristine)	?	?	Benzene Toluene	ND Trace	Brown *et al.*, 1979

[a] Total volatiles measured are comprised of 75% (benzene + toluene + xylenes); 25% other.
[b] Total six monocyclics: benzene, toluene, ethylbenzene and *p*-, *m*-, and *o*-xylenes.
[c] Unidentified: some presumably on estuaries.
ND = Not detected.

1 to 100 ppb, and in fresh water up to 200 ppb. Measurement units used for concentrations of MAH reported throughout this paper are as follows:

ppm=μl/L, ppb=nl/L in water; ppm=nl/g in tissues.

Tables 4 and 5 summarize types and concentrations of low-boiling point petrochemicals, including MAH, found in tissues of striped bass collected from the Carquinez Straits area of the San Francisco Bay-Delta (Whipple, 1979) during their upward spawning migration. As far as we know, there are no equivalent data for low-boiling point MAH for other fishes. Although traces of naphthalenes were present, few fish tissues examined contained significant levels of dicyclic aromatics. Other polycyclic aromatics (PAH) may be present, but tissue samples have not yet been analyzed for PAH. Our measurements of MAH in tissues of striped bass show surprisingly high concentrations (maximum in liver tissue=approx. 5.7 ppm; in ovary tissue=approx. 1.3 ppm; Table 5). The predominant monocyclic aromatic found is benzene. These concentrations closely approximate those resulting in tissues of fish exposed in the laboratory to 100 ppb of benzene (refer to Table 10). The initial data from field-captured fish are highly suggestive of a potential problem resulting from the occurrence of these compounds in a chronically polluted estuary, particularly in view of the effects observed at similar levels in laboratory studies.

RELATIONSHIP OF MONOCYCLIC AROMATIC HYDROCARBONS TO OTHER FACTORS IN THE AQUATIC ENVIRONMENT

As shown above, analyses of tissue samples from striped bass collected in the San Francisco Bay - Delta show the presence of MAH in relatively high concentrations (Whipple, 1979, 1980; Whipple *et al.*, 1979; Jung and Bowes, 1980). Although studies are still underway, we find that there are high correlations between the presence of these compounds and poorer condition of fish and their gametes. However, the cause and effect relationships between MAH and certain deleterious effects in the field-captured fish are as yet unclear, and laboratory tests are being performed in an attempt to clarify them.

Traditionally, much of the work on effects of petroleum hydrocarbons (including MAH) on aquatic organisms has been restricted to controlled laboratory studies, testing single compounds. This is primarily because of the difficulties in

TABLE 4. Low-boiling point petrochemicals scanned for in striped bass (*Morone saxatilis*) from San Francisco Bay; n=70 fish. Those compounds identified in striped bass liver tissue (total of 14 compounds) indicated with an asterisk. (Whipple, 1979, 1980; Whipple *et al*., 1979).

Aromatics	Alkyl cyclohexanes
*Benzene	*Methylcyclohexane
*Toluene	*1,4- and/or 1,1-Dimethylcyclohexanes
*Ethylbenzene	*1,2-Dimethylcyclohexane
**para*-Xylene	
**meta*-Xylene	
**ortho*-Xylene	
Isopropylbenzene	
n-Propylbenzene	
*1, 3, 5-Trimethylbenzene	
1, 2, 4-Trimethylbenzene, *tert*-Butylbenzene	
1, 2, 3-Trimethylbenzene, *sec*-Butlybenzene	
Isobutylbenzene	
n-Butylbenzene, 1-Phenylbutene-2	
tert-Pentylbenzene	
1, 2, 4, 5-Tetramethylbenzene	
1, 2, 3, 5-Tetramethylbenzene	
1, 2, 3, 4-Tetramethylbenzene	
*Naphthalene (Trace only)	
Hexylbenzene	
Pentamethylbenzene	
2-Methylnaphthalene	
*1-Methylnaphthalene (Trace only)	
n-Heptylbenzene	
Hexamethylbenzene	
n-Octylbenzene, *n*-Nonylbenzene	
Fluorene	
n-Decylbenzene	

TABLE 5. Summary of low-boiling point petroleum hydrocarbons in liver and gonads[a] in striped bass (*Morone saxatilis*). Prespawning adults; n=70; gonads maturing (Whipple, 1979; Whipple et al., 1979)

	Mean samples w/hydrocarbons (ppm-WW)	No. fish w/hydrocarbons detectable	No. fish without hydrocarbons (ND)	Total no. fish analyzed	Range in mean Low High (ppm-WW)
Liver tissue					
Females					
Total monocyclic aromatics[b]	0.430	46	10	56	0.020 - 3.285
Total alkyl cyclohexanes[c]	0.202	40	16	56	0.020 - 1.188
Total both	0.606	48	8	56	0.020 - 3.481
Males					
Total monocyclic aromatics	2.338	9	5	14	0.020 - 5.735
Total alkyl cyclohexanes	0.648	7	7	14	0.020 - 1.567
Total both	2.894	10	4	14	0.020 - 7.302
Gonadal tissue					
Females - Ovaries					
Total monocyclic aromatics	0.088	26	30	56	0.020 - 1.311
Total alkyl cyclohexanes	0.113	10	46	56	0.020 - 0.202
Total both	0.131	30	26	56	0.020 - 1.408
Males - Testes					
Total monocyclic aromatics	0.576	3	11	14	0.020 - 1.687
Total alkyl cyclohexanes	Trace	2	12	14	(Trace only)
Total both	0.589	3	11	14	0.020 - 1.707

ND = not detectable

[a] Data from 1978; fish from 1979 and 1980 being analyzed.

[b] Total monocyclic aromatics = Benzene + toluene + ethylbenzene + m-xylene + o-xylene; p-xylene undetectable.

[c] Total alkyl cyclohexanes = 1,4-dimethylcyclohexane + 1,1-dimethylcyclohexane + 1,2-dimethylcyclohexane.

testing complex mixtures of compounds such as occur in crude oil and petroleum fractions. It has been pointed out by Sprague (1971) and many others that laboratory studies are not necessarily indicative of what actually happens in the natural environment. The effect of any pollutant, or class of pollutants such as the MAH, on a fishery's population must ultimately be considered in relation to many other interacting variables before we can estimate its relative contribution to declines in the fishery. These variables may be naturally occurring (e.g., salinity) and/or man-introduced (e.g., pesticides). Fishes often migrate into or through estuaries with chronic levels of several different pollutants, probably interacting additively and/or synergistically with MAH and with natural factors.

An example of the probable interactions of various environmental factors affecting fish is shown in the conceptual model of Figure 2. This figure shows a portion of a qualitative model for the striped bass population in the San Francisco Bay - Delta, and postulates the effective variables and

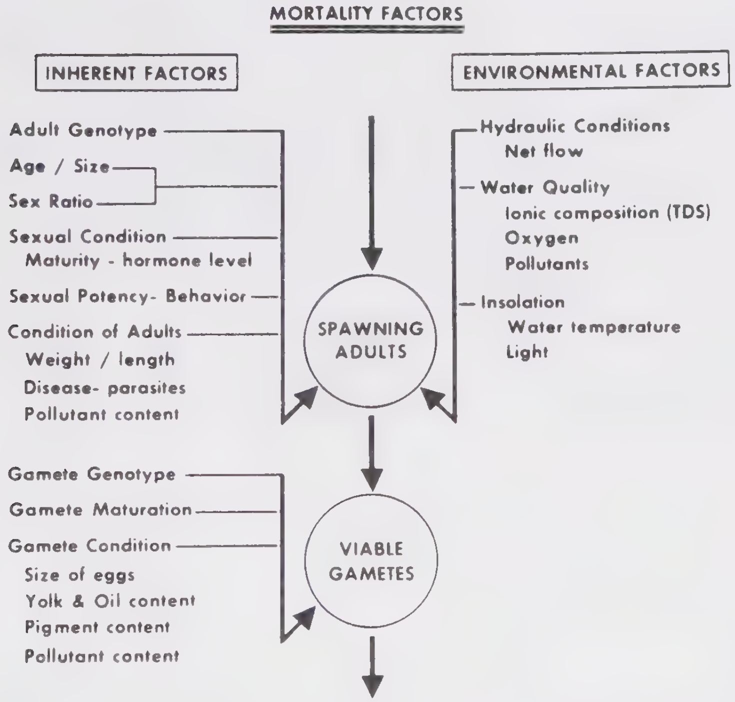

FIGURE 2. Conceptual model of factors affecting mortality in striped bass (Morone saxatilis) *during the spawning adult and gamete life history stages (from Whipple, 1979, 1980; Whipple* et al., *1979).*

their interactions affecting survival (or alternatively growth or reproduction) of a given life history stage (Whipple, 1979, 1980; Whipple *et. al.*, 1979). The stages shown in the figure are the spawning adults and their gametes. We believe these stages are among the most sensitive to the effects of pollutants. For this population, we are hypothesizing that pollutants, including MAH, are interacting with other environmental variables to affect adults and their gametes. Our ultimate goal is to make this model quantitative and predictive, determining the relative contribution of pollutants to reducing survival, growth and reproduction in the population considered. Very little has been done to quantify pollutant effects on a population in the actual environment where pollutants may be a probable factor in population persistence.

Although we would like ultimately to be able to predict effects of MAH on fishes in the aquatic environment, until further field and laboratory work has been done on their interaction with other factors, such prediction will be difficult. Data are available, however, from several studies on bioaccumulation and effects of MAH in fishes (primarily benzene and toluene). These studies enable us to make some preliminary predictions on the effects of MAH on fishes in the natural environment.

One of the difficulties in using data available from laboratory experiments to predict effects in the field, is that studies have been done under variable conditions. For example, we believe that fishes possess considerable interspecific and intraspecific inherent variability in their responses to pollutants, and environmental variability complicates this situation further. Table 6 lists some selected variables which we hypothesize will influence bioaccumulation of MAH in both field and laboratory studies and, subsequently, effects of these compounds on fishes. The point of listing these sources of variability is to provide a framework for future laboratory studies, where variation can be controlled or eliminated.

Further discussion of the influence of the variable listed in Table 6 on uptake, retention and depuration of MAH follows.

UPTAKE AND ACCUMULATION OF MONOCYCLIC AROMATIC HYDROCARBONS

The major route of uptake for MAH in fishes is probably through the water column, although this is not the only potential source of exposure to MAH (Table 6). Few studies exist comparing the routes of uptake and their relative importance in the bioaccumulation of MAH in fishes. We have done studies comparing the bioaccumulation of benzene in Pacific herring

TABLE 6. Some inherent and environmental variables affecting uptake, metabolism, retention and effects of MAH on fishes. Some factors (*) are still hypothetical, although currently being tested (Whipple, 1979, 1980; Whipple _et_ _al_., 1979).

Major Inherent Factors	Major Environmental Factors
Interspecific variability (Table 9)	Source of exposure (Tables 7, 8) Water, food, particulates, or sediments, or combinations of these
Sex (Table 5)	Type of component or component mixture (Table 11)
Life history stage (Tables 7, 8, 9, 11)	Concentration, length of exposure (Tables 9, 11)
*Intraspecific genotypic variability Metabolism - functional Structural	
	Temperature (Table 11)
*Condition when exposed Degree of disease or parasitism Previous feeding regime - amount of fat Existing pollutant load	Salinity (Table 11)
	Alkalinity - pH (Table 11)
	*Presence of other pollutants Chlorinated hydrocarbons Heavy metals Others

Laboratory experiments can reduce this variability to a considerable degree by controlling (fixing) the variability and thus maximizing the variation due to effects of test (treatment) components.

In field experiments, more variables are uncontrollable and sample sizes must be larger, to reveal differences between exposed and unexposed populations.

larvae exposed from the water only, food only (contaminated rotifers) and water and food together (Eldridge and Echeverria, 1977). We have also compared the uptake and bioaccumulation of the components in the WSF of Cook Inlet crude oil in starry flounder exposed through water only, food only (contaminated clams) and both water and food (Whipple *et al.*, 1978a; also Yocom *et al.*, ms in prep.). Summaries of concentrations accumulated from different exposure sources are shown in Tables 7 and 8. Our general conclusion from studies done to date is that only trace amounts of MAH are taken up from contaminated food and that, in fish, bioaccumulation of these compounds probably does not occur from food. There are no studies of the potential bioaccumulation from other sources (e.g., particulates).

A number of studies (discussed below), however, show that MAH are readily and rapidly bioaccumulated from water. We believe that this is the major route of uptake in the field, and that the source of exposure is most likely to be a low concentration (1-100 ppb, occasionally higher) of MAH occurring chronically in polluted estuaries.

The rates of uptake of MAH, particularly benzene, are very rapid. Figure 3 shows uptake of benzene in the blood of striped bass exposed to approximately 1 ppm benzene (Benville *et al.*, 1980). Other studies show that uptake to maximum equilibrium levels in most tissues is reached within 2-24 hrs (Korn *et al.*, 1976a, 1977). Maximum levels in organs involved with metabolism of MAH are reached later (48-72 hrs). In longer exposures, such as in starry flounder exposed to the WSF of Cook Inlet crude oil in the laboratory, the order of magnitude of accumulation remained the same over the entire exposure period once equilibrium levels were reached (Figure 4). There was some indication of increased accumulation at about five weeks.

Tables 9 and 10 summarize the concentrations and bioaccumulation of benzene and toluene in fishes. Data are summarized to compare species, life history stages and tissues. Most data are from laboratory experiments (L); however, some field data (F) are also included for comparison.

Test concentrations of single components (benzene and toluene) varied from 1 ppb to approximately 10,000 ppb (0.001 - 10.000 ppm). The 10,000 ppb (10 ppm) level was near lethal for some species. Most test concentrations of both single components and total MAH, however, were approximately 100 ppb and were chosen to approximate field chronic levels. Data from field-captured striped bass (F) show that maximum accumulation of benzene is comparable to that in striped bass exposed to approximately 100 ppb in the laboratory. Except at the lowest and highest test concentrations (1 ppb and 10,000 ppb), the order of magnitude of accumulation in juvenile and

TABLE 7. Mean maximum concentrations of benzene and/or metabolites in herring larvae (*Clupea harengus pallasii)* exposed to ^{14}C-benzene in seawater and/or in food (rotifers; *Brachionus plicatilis)* for 72 hours (Eldridge and (Echeverria, 1977).

Initial Mean Benzene Concentration (ppm-µl/L)	Concentrations in Tissues - ppm; nl/g Wet Weight		
	Food + Water Exposure	Water Only	Food Only
0.144 - 2.10		0.49 - 8.16	
1.20	3.98		
1.20 (rotifers)			0.310

TABLE 8. Mean concentrations of different classes of petroleum hydrocarbons in some tissues of starry flounder (*Platichthys stellatus)* exposed to a total of 0.115 ppm MAH in the WSF of Cook Inlet crude oil and/or 8.0 ppm MAH in contaminated clams (*Tapes semidecussata)* for five weeks in the laboratory (Whipple et al., 1978a; also Yocom et al., ms in prep.). Control group (not shown) contained no detectable components.

Component Class Totals	Concentrations in Tissues (ppm; µg/g-WW)					
	Food + Water Exposure		Water Only		Food Only	
	Mean	n	Mean	n	Mean	n
Liver						
Alkyl cyclohexanes	26.45	22	30.38	20	1.22	21
*Monocyclic aromatics	19.53	22	21.44	20	0	21
Higher substituted benzenes	23.89	14	16.17	15	0	13
Dicyclic aromatics	10.15	14	8.37	15	0	13
Muscle						
Alkyl cyclohexanes	0.88	23	0.50	24	0	18
Monocyclic aromatics	1.04	23	0.60	24	0	18
Higher substituted benzenes	0.92	20	2.03	22	trace m-xylene	8
Dicyclic aromatics	0.30	20	0.31	22	0	8

*Monocyclic aromatics = Six most common in WSF of Cook Inlet Crude Oil; benzene, toluene, ethylbenzene, o-xylene, m-xylene, p-xylene.

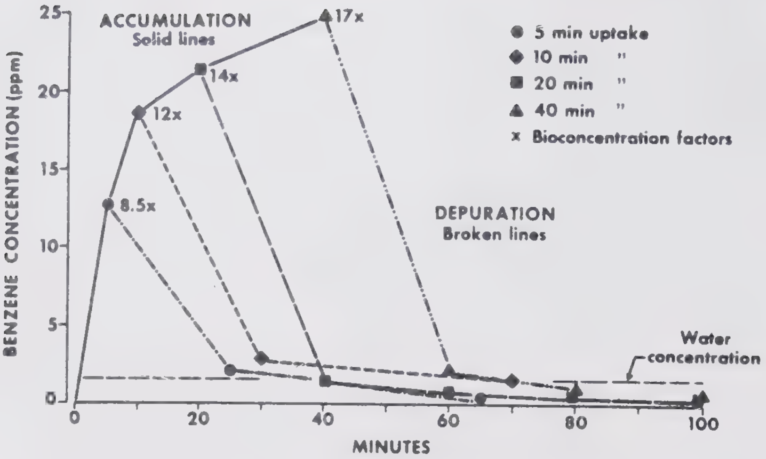

FIGURE 3. Uptake, accumulation and depuration of benzene in blood of striped bass (Morone saxatilis) exposed to approximately 1.0 ppm benzene through the water column for one hour (from Benville et al., 1980).

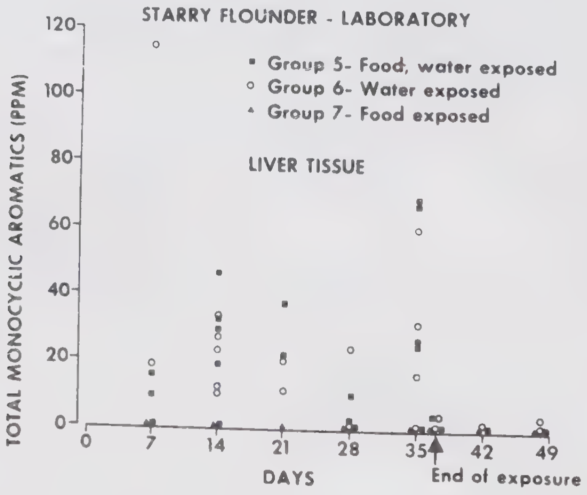

FIGURE 4. Uptake, accumulation and depuration of six common monocyclic aromatic hydrocarbons in the WSF of Cook Inlet crude oil in the liver tissue of starry flounder (Platichthys stellatus). Exposed to 0.100 ppm total MAH in the WSF of Cook Inlet crude oil through the water column for five weeks (from Yocom et al., ms in prep.; Whipple et al., 1978a).

adult fishes was the same in most species (water concentration from 10 to 5,000 ppb), being about 10 to 100 times the water concentration (8.3 to 140 X). Maximum accumulation of benzene, as a part of the WSF of crude oil, appeared to be of the same order of magnitude as of benzene alone. Maximum accumulation of total MAH in the WAF appeared to be approximately 100 times water concentrations in laboratory studies (1 to 350 X). Toluene accumulated to higher levels than did benzene in most laboratory studies, depending upon tissue.

When tissues and species were compared (Table 10), northern anchovies accumulated the highest concentrations, probably because these fish were more easily stressed by laboratory conditions. Lowest accumulation occurred in Pacific herring. The other species had approximately the same maximum accumulations.

Accumulation of MAH varied with sex and proximity of males and females to spawning (Whipple, 1979). In striped bass during spawning season, benzene and other MAH were approximately equally distributed between liver and ovaries in females. Accumulation in males was higher in liver and levels in testes were usually undetectable, some with a trace of toluene. During the nonspawning season, levels were higher in female tissues, including liver, than in male. The levels in liver and gonads were probably largely determined by the amount of stored lipid, with increasing amounts of lipid being transferred from the liver to the ovaries during vitellogenesis. A corresponding change apparently does not occur in males during the spawning season. The rest of the year, female livers are higher in lipid than male livers. When data are pooled for all species and stages of juveniles and adults, females show higher accumulation (40 X) than males (26 X).

Differences among life history stages for Pacific herring, striped bass, starry flounder and coho salmon are also summarized in Table 9. Accumulation in early life history stages of striped bass was higher than in Pacific herring and coho salmon, particularly in feeding larvae. Maximum accumulation of ^{14}C-benzene and metabolites occurred in feeding larvae of striped bass (1400 X at 384 hrs and still increasing). Gonadal eggs also reached fairly high levels when maturing (14-29 X). Generally, in striped bass, the different stages bioaccumulate in the following, increasing order: yolk-sac larvae, nonspawning adults and juveniles, gonadal eggs, spawned eggs, prespawning adults, nonfeeding post yolk-sac larvae and feeding post yolk-sac larvae. In starry flounder, the order of increasing bioaccumulation is as follows: immature ovaries, juveniles, nonspawning adults,

TABLE 9. Summary of mean concentrations and bioaccumulations of benzene and toluene in different species and life history stages. Most experiments were at an exposure level of approximately 0.100 ppm.

		Benzene			Toluene			
Variable	Water exposure level (ppm)	Range - Mean maximum concentrations[a] (ppm)	Maximum accumulation factor[b]	Hours to maximum accumulation	Range - Mean maximum concentrations[a] (ppm)	Maximum accumulation factor[b]	Hours to maximum accumulation	References
Species and Life history stages								
Starry flounder								
Gonadal eggs								
Immature	L 0.133 B^c							
	L 0.088 T^c	ND	No accum.	--	0.200-0.830	9.4x	504	Whipple et al., 1978b
Mature	L 0.047 B^c							
	L 0.056 T^c	1.18-1.86	39x	72-96	2.16 - 5.21	93x	72-96	Whipple et al., 1978b
Juveniles	L 0.133 B^c							
	L 0.088 T^c	4.61-18.60	140x	504	14.24-34.71	395x	504	Whipple et al., 1978b
Nonspawning adults	L 0.041 B^c							
	L 0.043 T^c	0.130-4.19	100x	840	0.420-8.90	205x	840	Yocom et al., ms in prep.;
Prespawning adults	L 0.047 B^c							Whipple et al., 1978a
	L 0.056 T^c	1.44-1.57	33x	72-96	3.19-4.61	82x	72-96	Whipple et al., 1978b
Coho salmon								
Spawned eggs	*L 1.80 T				8.10	4.5x	unknown	Korn and Rice, in press
Alevins	*L 1.80 T				2.70	1.5x	unknown	Korn and Rice, in press
Emergent fry	*L 1.80 T				6.70	3.7x	unknown	Korn and Rice, in press
Pacific herring								
Gonadal eggs								
Immature	*L 0.100 B							
	*L 0.100 T	0.240	2.4x	24	0.440	4.4x	6	Korn et al., 1977
Mature	*L 0.100 B	1.40	14.0x	24				Struhsaker, 1977
Spawned eggs	*L 0.100 B	0.600	6.0x	12				Struhsaker, 1977
Feeding larvae								
Fed	*L 0.100 B	0.700	7.0x	not rchd 72				Struhsaker, 1977
Fed	*L 0.140 B	0.250	1.8x	not rchd 72				Eldridge and Echeverria, 1977
Not fed	*L 0.144 B	0.230	1.6x	6				Eldridge and Echeverria, 1977
Nonspawning adults	*L 0.100 B							
	*L 0.100 T	0.830	8.3x	6-48	3.90	39x	6-72	Korn et al., 1977

Variable	Water exposure level (ppm)	Benzene			Toluene			References
		Range - Mean maximum concentrations[a] (ppm)	Maximum accumulation factor[b]	Hours to maximum accumulation	Range - Mean maximum concentrations[a] (ppm)	Maximum accumulation factor	Hours to maximum accumulation	
Striped bass								
Gonadal eggs (mature)	F (?)[d]	Trace only	No. accum.	chronic	Tr.-0.330	(3.3x)[d]	chronic	Whipple, 1979, 1980
Spawned eggs	*L 0.138	4.512	33x	33				Eldridge and Benville, ms in prep.
Yolk-sac larvae	*L 0.415	4.674	11x	120				Eldridge and Benville, ms in prep.
Feeding larvae								
Fed	*L 0.159	226.155	1400x	not rchd 384				Eldridge and Benville, ms in prep.
Not fed	*L 0.159	73.663	460x	360				Eldridge and Benville, ms in prep.
Juveniles	*L 0.088	1.302	15x	6				Korn et al., 1976a
Nonspawning adults	L 0.095	4.35	46x	336				Hirsch et al., ms in prep. (b)
	F(0.100)[d]	Tr.-4.58	(46x)[d]	chronic	0	No toluene, only benzene		Whipple et al., ms in prep.
Prespawning adults	L 0.750	2.0-20.0	27x	336				Hirsch et al., ms in prep. (b)
	F(0.100)[d]	Tr.-2.27	(23x)[d]	chronic	Tr.-0.330	?	chronic	Whipple et al., ms in prep.

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*Indicates labeled compounds (accumulation of ^{14}C-benzene or ^{14}C-toluene + their metabolites, if any).

L = accumulation in laboratory-exposed fish. B = benzene.

F = accumulation in field-captured fish. T = toluene.

[a] Measurement of uptake in bile not included in mean maximum concentrations.

[b] Maximum accumulation factor = Mean maximum concentration of MAH in tissues divided by mean concentration in water column.

[c] WSF of Cook Inlet crude oil.

[d] If comparable to laboratory accumulation, approx. 0.100 ppm benzene in field.

TABLE 10. Summary of mean maximum concentrations and bioaccumulation of benzene in different species, tissues and sexes. Most experiments were at an exposure of approximately 100 ppb.

Tissues - Species[a]		Water Exposure Level (ppm)	Mean Maximum Concentration (ppm)	Maximum Accumulation Factors (Increasing order)
Gonads (Immature)				
Pacific Herring (A)	(*)	0.100	0.240	2.4 x
Striped Bass (A)	(-)	0.320	Trace	None
Stomach				
Striped Bass (J)	(*)	0.088	0.24	2.7 x
Testes (Mature)				
Striped Bass (A)	(-)	0.320	1.09	3.4 x
Heart				
Striped Bass (J)	(*)	0.088	0.26	2.9 x
Striped Bass (A)	(-)	0.320	1.82	5.7 x
Kidney				
Pacific Herring (A)	(*)	0.100	0.40	4.0 x
Striped Bass (A)	(-)	0.320	4.16	13 x
Pyloric Cecae				
Pacific Herring (A)	(*)	0.100	0.64	6.4 x
Colon				
Striped Bass (J)	(*)	0.088	1.32	15 x
Spleen				
Striped Bass (A)	(-)	0.320	6.40	20 x
Adrenal Gland				
Striped Bass (A)	(-)	0.320	6.72	21 x
Eye				
Striped Bass (A)	(-)	0.320	7.68	24 x
Blood				
Striped Bass (A)	(-)	0.320	8.64	27 x
Ovaries (Mature)				
Pacific Herring (A)	(*)	0.100	1.40	14 x
Striped Bass (A)	(-)	0.100	2.90	29 x
Muscle				
Striped Bass (J)	(*)	0.088	0.10	1.1 x
Pacific Herring (A)	(*)	0.100	0.63	6.3 x
No. Anchovy (A)	(*)	0.110	1.10	10 x
Striped Bass (A)	(-)	0.320	0.48	1.5 x

Table 10 con't.

Gills				
Striped Bass (J)	(*)	0.088	0.49	5.6 x
Pacific Herring (A)	(*)	0.100	0.73	7.3 x
No. Anchovy (A)	(*)	0.110	4.60	42 x
Brain				
Striped Bass (J)	(*)	0.088	0.63	7.2 x
Pacific Herring (A)	(*)	0.100	0.75	7.5 x
No. Anchovy (A)	(*)	0.110	4.60	42 x
Striped Bass (A)	(-)	0.320	7.36	23 x
Liver				
Striped Bass (J)	(*)	0.088	0.86	9.8 x
Pacific Herring (A)	(*)	0.100	0.53	5.3 x
No. Anchovy (A)	(*)	0.110	6.01	55 x
Striped Bass (A)	(-)	0.320	6.72	21 x
Mesenteric Fat				
Striped Bass (A)	(-)	0.320	35.0	109 x
Intestine				
Striped Bass (J)	(*)	0.088	0.48	5.4 x
Pacific Herring (A)	(*)	0.100	0.83	8.3 x
No. Anchovy (A)	(*)	0.110	22.9	210 x
Gall Bladder (Bile)				
Pacific Herring (A)	(*)	0.100	3.10	31 x
Striped Bass (J)	(*)	0.088	4.70	53 x
No. Anchovy (A)	(*)	0.110	480.	4400 x
Striped Bass (A)	(-)	0.320	3.80	12 x

---

[a] References: Korn *et al.*, 1976a, 1977; Hirsch *et al.*, ms. in prep.(b); Struhsaker, 1977.

(-) Benzene not labeled; (*) ^{14}C-Benzene and/or metabolites; (A) = Adult, (J) = Juvenile.

prespawning adults and mature ovaries (egg and larval stage studies incomplete). Alevins of coho salmon accumulated more than spawned eggs or emergent fry.

Tissues accumulating highest levels were those involved in metabolism of compounds (^{14}C-benzene and metabolites measured) and/or contained higher levels of lipids. The tissues are arranged in order of minimum to maximum accumulations, the least uptake occurring in testes and the highest in bile (Table 10). In muscle, liver and bile, measurements were made of both 1) ^{14}C-benzene and metabolites and 2) benzene only. In the case of bile, a considerably higher proportion of the measured concentration appears to be metabolites.

The uptake of benzene and toluene as a part of the WSF of Cook Inlet crude oil by starry flounder appeared to be slightly higher than uptake and accumulation of the individual compounds, e.g., benzene in other species (Table 9). This could be a species difference, however.

Figure 5A is a gas chromatogram showing the occurrence

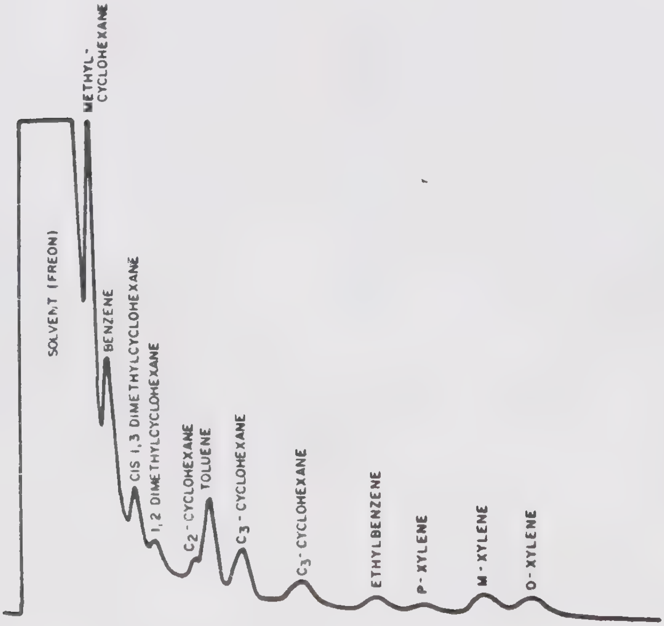


FIGURE 5A. Chromatogram of low-boiling point hydrocarbons, including monocyclic aromatic hydrocarbons, detected in a maturing ovary of starry flounder (Platichthys stellatus). Exposed to 0.115 ppm total MAH in the WSF of Cook Inlet crude oil for seven days (from Whipple et al., 1978b).

of the low-boiling point compounds of methylcyclohexanes and monocyclic aromatics in maturing ovarian tissue of starry flounder exposed to the WSF of Cook Inlet crude oil (Whipple *et al.*, 1978b). Highest concentrations were of methylcyclohexane and benzene, but relative accumulations differed because of the much lower concentrations of xylene in the water. Figure 5B shows the relative uptake of different classes of hydrocarbons in the WSF of Cook Inlet crude oil in ovaries of starry flounder. Concentrations of the six commonest monocyclics (M-1) were highest, followed by methylcyclohexanes (CH), other substituted benzenes (M-2), and finally by dicyclic aromatic hydrocarbons (D). Although the MAH accumulate in fishes to relatively high concentrations from the WSF, the relative toxicities of these classes of compounds differ and effects cannot be determined on the basis of concentration alone.

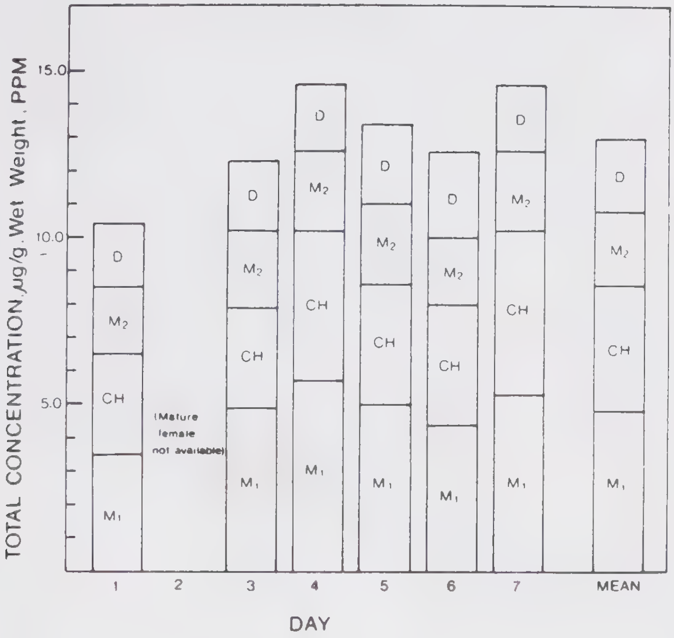


FIGURE 5B. Concentrations of monocyclic aromatics and other compounds in maturing ovaries of starry flounder (Platichthys stellatus). *M1 = six common monocyclics (benzene, toluene, ethylbenzene,* p-, m-, *and* o-*xylenes); CH = total alkyl cyclohexanes; M2 = total higher substituted benzenes; D = total dicyclic aromatics. Exposed to 0.115 ppm total MAH in the WSF of Cook Inlet crude oil for seven days (from Whipple* et al., *1978b).*

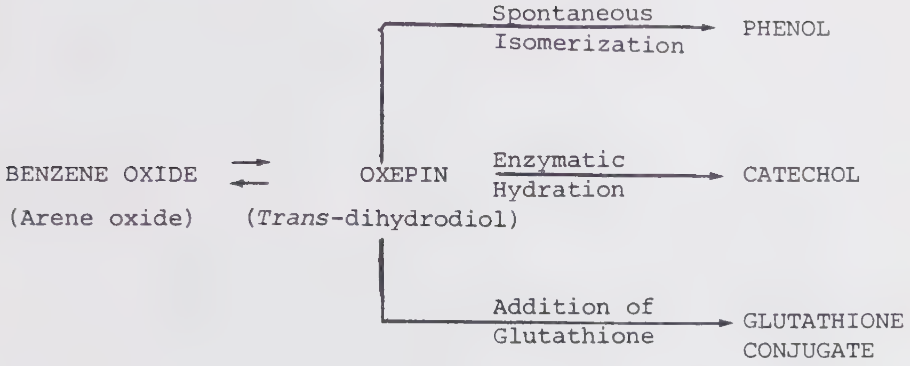
METABOLISM

Although we know that uptake of MAH from water is very rapid, and that bioaccumulation above water concentrations occurs, we still do not know much about what happens to these compounds within the fish. A considerable amount of the MAH taken up is probably returned to the water through the gills, unchanged. Some, however, is probably metabolized (Korn *et al.*, 1976a, 1977).

Fish have oxidative enzyme systems for the metabolic detoxification of xenobiotics, including the aromatic petroluem hydrocarbons (Payne and Penrose, 1975). They are associated with microsomes in the endoplasmic reticulum of cells. These enzymes are NADPH-dependent, and called aryl hydrocarbon hydroxylases (AHH). This area of research is relatively new (1960's to present) and information on the metabolic detoxification of petroleum hydrocarbons in fish is still sparse. Research on mammals is summarized in the papers of LaDu *et al.* (1971), White *et al.* (1973), Jerina and Daly (1974) and Kappas and Alvares (1975). Recently, considerable work has been done on the metabolism of polycyclic aromatics (PAH) in fishes (Lee, 1976, 1977; Stegeman and Sabo, 1976; Malins, 1977a, 1977b; Neff, 1978a, 1978b, 1979; Varanasi and Malins, 1977). There is still little known, however, about the metabolism of MAH in fish. Gibson (1977) summarized the differences in the metabolic processes used by eucaryotic and procaryotic organisms to oxidize aromatic hydrocarbons, including monocyclic aromatics such as benzene and toluene. Bacteria apparently oxidize MAH to dihydrodiol intermediates, followed by formation of catechols. The catechols are then substrates for the enzymatic cleavage of the aromatic ring. Fungi and higher organisms, on the other hand, incorporate oxygen into the aromatic ring to form arene oxides. The oxides undergo enzymatic addition of water to yield *trans*-dihydrodiols. These, in turn, are transformed into phenol, catechols and glutathione conjugates, according to Jerina and Daly (1974).

Most of the studies indicate a basic similarity of aromatic detoxification in mammals and fishes, including evidence that the mixed function oxidases (MFO) are induced in fish exposed to petroleum (Stegeman and Sabo, 1976; Payne and Penrose, 1975).

Jerina and Daly (1974) summarized the hepatic metabolism of benzene in mammals. Studies show that under physiological conditions (*in vitro*), benzene oxide undergoes spontaneous rearrangement to form phenol and react nonenzymatically with the thiol group of glutathione. Benzene oxide also undergoes enzymatic hydration to catechol. The general reactions are as follows:



The rate of metabolism of benzene *in vitro* was relatively low and the arene oxides of benzene and alkylbenzenes very unstable. The hepatic metabolism of toluene and other aromatics is also described in Jerina and Daly (1974). The hepatotoxicity of these compounds in mammals is apparently caused by the arene oxides being covalently bound to hepatic protein, eventually resulting in necrosis. Addition of glutathione inhibits this process.

We do not know if the same process of metabolism of benzene occurs in fishes, but similarities in the MFO system suggest that it does. Roubal *et al.* (1977) compared the accumulation and metabolism of ^{14}C-labeled compounds (benzene, naphthalene and anthracene) in young coho salmon exposed through food and intraperitoneal injection. Although the metabolites of benzene were not identified, the results show that relative to naphthalene and anthracene, a lower proportion of the ^{14}C-activity of labeled benzene appeared in the form of metabolites at 24 hours in the tissues measured (brain, liver, gall bladder, flesh and carcass). Overall, the accumulation of ^{14}C-labeled benzene and metabolites was less than for ^{14}C-labeled naphthalene and anthracene. The paper also indicated that for naphthalene and anthracene, maximum ^{14}C-activity levels were lower and depuration slower when labeled compounds were administered via food as opposed to injection.

Studies of striped bass juveniles indicated that in liver and muscle tissue approximately half of the ^{14}C-labeled compounds were unchanged benzene and half in the form of metabolites when compared to gas chromatographic measurements of unchanged benzene (Korn *et al.*, 1976a, 1977; see also Table 10). In the gall bladder, however, most of the labeled material in bile was probably metabolites, as would be expected.

A recent study (Thomas and Rice, in press) examined the excretion of ^{14}C-labeled toluene and naphthalene from the gut of Dolly Varden char. Results showed that the major avenue for excretion of the parent hydrocarbons and their metabolites was via the gills, and minor portions were excreted via the gut and kidney. Most excretion via the gill was still in the form of the parent hydrocarbons; most excreted via the gut and kidney were in the metabolite phase.

The MAH bear structural similarity to many natural compounds such as steroid hormones, lipids, vitamins and neurotransmitters which also contain aromatic nuclei. This similarity may result in competition with other substrates for metabolism in the MFO system (LaDu *et al.*, 1971). MAH may also mimic effects of natural compounds, stimulating certain neuroendocrine responses and behavior (Doggett *et al.*, 1977; LaDu *et al.*, 1971). More research in this area would be of considerable interest.

TRANSLOCATION

Based on the above studies, we propose that the translocation of MAH through fish occurs as diagrammed in Figure 6. The major route of uptake is from water through the gills. Some uptake may be through the gut from swallowed water, particularly in salt water environments. A minor portion, if any, is taken through the intestinal wall. Most data indicate a minimal uptake of MAH through food (see Tables 7 and 8; Figure 4). The parent compounds readily solubilize in cell membranes (Roubal, 1974; Roubal and Collier, 1975) and are probably carried primarily via the erythrocytes (lipid cell membrane) through the general circulation in the blood (Benville *et al.*, 1980; Figure 3). Some of the monocyclics may also be carried by lipoproteins and leukocytes in the blood. Centrifugation of blood from benzene-exposed striped bass showed that the major portion of the benzene was associated with the erythrocytes, and not the serum fraction (Hirsch *et al.*, ms in prep. (b)). The blood circulates through the fish, and the aromatics apportion into target tissues and organs (Fig. 7) that have high lipid content (e.g., brain) (Korn *et al.*, 1976a, 1977). They are also transported to the liver where they are metabolized (some limited metabolic activity in other tissues is also possible). Benzene and metabolites are then both transported through the general circulation, where they reenter target tissues or are depurated. A considerable portion of the unchanged compounds probably diffuses back through the gills into the water. The

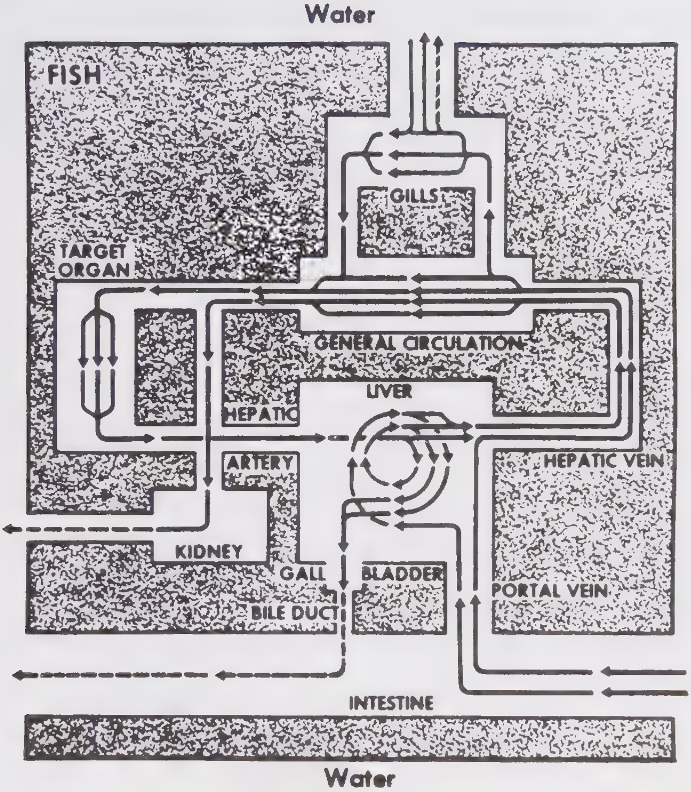


FIGURE 6. Translocation of monocyclic aromatic hydrocarbons and their metabolites in fish exposed through the water column. Dashed lines indicate routes for excretion of metabolites (adapted from Kappas and Alvares, 1975).

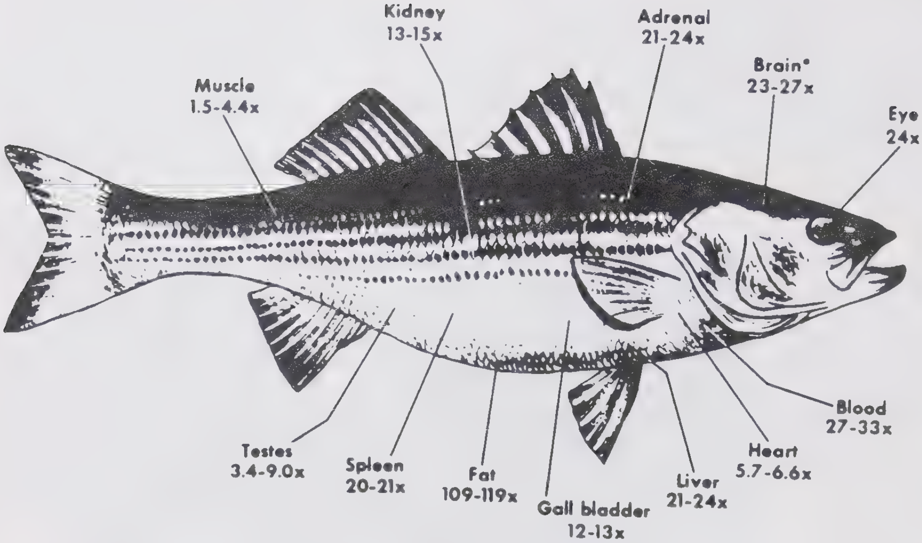


*FIGURE 7. Bioaccumulation of benzene in different tissues of the striped bass (*Morone saxatilis*) exposed to approximately 1.0 ppm benzene through the water column (from Benville* et al., *1980).*

major route of excretion of metabolites appears to be via the bile into the intestine and out with the feces. Some metabolites are excreted through the gills. A minor portion of metabolites appears to pass through the kidney. At high exposure levels of MAH, the metabolic detoxification capacity of the liver may be exceeded and higher concentrations of unchanged compounds probably accumulate in the target organs.

DEPURATION

MAH are depurated relatively rapidly, parent compounds usually disappearing from most tissues within 48 hrs (e.g., Figs. 3 and 4), although the rate of disappearance is slower than the rate of uptake in most tissues (Fig. 3). The depuration of metabolites takes longer and persistence in tissues involved with metabolism is greater (Korn *et al.*, 1976a, 1977). In striped bass, Pacific herring and northern anchovy, residues of benzene/metabolites were detected in gills, liver and gall bladder seven days after termination of exposure. These organs, of course, are involved with metabolism and excretion of metabolites. In addition, residues were still detectable in fat tissue seven days after termination of exposure.

UPTAKE, ACCUMULATION AND DEPURATION IN LARVAL FISH

Adult and juvenile fishes appear to accumulate MAH very rapidly and to relatively high equilibrium levels within 24 hrs. The unchanged parent compounds are also rapidly depurated, although metabolites may persist for longer periods.

Larval fish, however, appear to have limited capacity to either metabolize or excrete ^{14}C-benzene. Table 9 and Figure 8 show some of the results of an experiment in which striped bass larvae were exposed to ^{14}C-labeled benzene from the water column in a semi-static system. Benzene was added daily to restore a test concentration of approximately 120 ppb benzene (Eldridge and Benville, ms in prep.). Figure 8 shows that the uptake of benzene in feeding larvae fed uncontaminated *Artemia* nauplii was higher than in starved larvae. The major route of uptake is still through water, but when larvae are actively feeding, they appear to continually accumulate benzene and/or metabolites more than when starved. Concentrations were still increasing 16 days after initiation of feeding (Day 24). Possible explanations for this are: 1) larvae have limited enzymatic capacity to metabolize benzene and thus accumulate benzene to high levels (at least 1400 X water concentration) or 2) larvae are unable to excrete accumulated metabolites or 3) both of these. The first explanation seems most plausible. Fetuses and young of mammals also have extremely limited capacity to metabolize aromatic hydrocarbons and other drugs (LaDu *et al.*, 1971).

EFFECTS OF MONOCYCLIC AROMATICS

Acute Toxicity

The bioaccumulation of selected MAH in fishes was summarized previously (Tables 9 and 10). Generally, the effects of MAH will depend upon their concentration in fish and deposition in specific target organs and tissues. For example, the species, stages and tissues which accumulate highest levels, under most conditions, will be most sensitive to MAH; those bioaccumulating less generally will be least sensitive. The effects at a given concentration, however, will also vary according to other inherent and environmental variables as previously discussed and listed in Table 6.

The acute toxicity (96-hr LC_{50}'s) of MAH to fishes ranges from about 2.0 to 300 ppm (Table 11). When the toxicities of

Table 11. Acute bioassays of single monocyclics and for comparison, of water-soluble fraction (WSF) of oil containing monocyclics and other compounds.

Exposed Species/Stage	Salinity Temperature	System[a]	Compound	Concentration (ppm)	Effect (LC$_{50}$)[b] (TLm)[c]	References
Clupea harengus pallasi						Struhsaker et al., 1974
Pacific herring,						
Eggs through early cleavage (survival to hatching)	24 ppt SW 15.2°C	Semi-Static	Benzene	40-45	96h[b]	
Larvae 2 days after hatching	28 ppt SW 12.9°C	Semi-Static	Benzene	20-25	48h[b]	
Engraulis mordax						Struhsaker et al., 1974
Northern anchovy						
Eggs to hatching larvae (survival to hatching)	28 ppt SW 17.5°C	Semi-Static	Benzene	20-25	48h[b]	
Oncorhynchus kisutch						Korn & Rice, (In press)
Coho salmon						
Eggs	0 ppt FW 3.5-6°C	Semi-Static	Toluene	333	96h[b]	
(Hatching)				100	96h[b]	
Alevins						
Early				60	96h[b]	
Middle				20	96h[b]	
Late				9.36	96h[b]	

Eggs hatching	0 ppt FW 3.5-6°C	Semi-Static	Naphthalene	11.8	96h[b]	
Alevins						
Early				9	96h[b]	
Middle				8	96h[b]	
Late				4	96h[b]	
Emergent fry				2-3	96h[b]	
Oncorhynchus tshawytscha Chinook salmon Juveniles	0 ppt FW 6°C	Semi-Static	WSF of Prudhoe Bay crude oil	3.59	96h[c]	Moles *et al.*, 1979
	9°C		Benzene	11.73	96h[c]	
Oncorhynchus kisutch Coho salmon	0 ppt FW 8°C	Semi-Static	WSF of Prudhoe Bay crude oil	3.67	96h[c]	Moles *et al.*, 1979
	9°C		Benzene	14.09	96h[c]	
Coho Salmon Juveniles	30 ppt SW 8°C	Static	Benzene	10-50	96h[b]	Morrow, 1974
			Toluene	10-50	96h[b]	
			Ethylbenzene	10-50	96h[b]	
			Xylene	10-100	96h[b]	

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[a] Systems: Static - Initial dose only, declining over test period; Semi-static - Daily addition to bring test concentration up to dose level over test period; Open flow - Constant exposure to open flow system of test concentrations.

SW = seawater; FW = fresh water

Table 11 con't.

Exposed Species/Stage	Salinity Temperature	System^a	Compound	Concentration (ppm)	Effect $(LC_{50})^b$ $(TLm)^c$	References
Oncorhynchus gorbuscha Pink salmon Juveniles	26-30 ppt SW $3.7-11^{o}C$	Semi-Static	WSF of Cook Inlet crude oil	4.13 2.92	$24h^c$ $96h^c$	Rice *et al.*, 1976
			WSF of #2 fuel oil	0.89 0.81	$24h^c$ $96h^c$	
Pink Salmon Smolts	0 ppt FW $4^{o}C$	Semi-Static	WSF of Prudhoe Bay crude oil	7.99	$96h^c$	Moles *et al.*, 1979
	28-30 ppt SW $4^{o}C$		WSF of Prudhoe Bay	3.73	$96h^c$	
	0 ppt FW $4^{o}C$	Semi-Static	Benzene	17.09	$96h^c$	
	28-30 ppt SW $4^{o}C$		Benzene	8.47	$96h^c$	
Oncorhynchus nerka Sockeye salmon Smolts	0 ppt FW $6^{o}C$	Semi-Static	WSF of Prudhoe Bay crude oil	2.22	$96h^c$	Moles *et al.*, 1979
	28-30 ppt SW $6^{o}C$		WSF of Prudhoe Bay crude oil	1.05	$96h^c$	
Sockeye Salmon Smolts	0 ppt FW $6^{o}C$	Semi-Static	Benzene	10.76	$96h^c$	
	28-30 ppt SW $6^{o}C$		Benzene	5.55	$96h^c$	

Salvelinus malma Dolly Varden Juveniles	0 ppt FW 8°C	Semi-Static	WSF of Prudhoe Bay crude oil	2.75	$96h^c$	Moles *et al.*, 1979
			Benzene	11.96	$96h^c$	
Smolts	0 ppt FW 8°C	Semi-Static	WSF of Prudhoe Bay crude oil	2.68	$96h^c$	
	28-30 ppt SW 8°C	Semi-Static	WSF of Prudhoe Bay crude oil	1.38	$96h^c$	
	0 ppt FW 8°C	Semi-Static	Benzene	11.90	$96h^c$	
	28-30 ppt SW 8°C		Benzene	6.30	$96h^c$	
(Dolly Varden) Smolts	26-30 ppt SW 3.7-11°C	Semi-Static	WSF of Cook Inlet crude oil	3.25 2.94	$24h^c$ $96h^c$	Rice *et al.*, 1976
			WSF of #2 Fuel Oil	2.29	$96h^c$	

Table 11 con't.

Exposed Species/Stage	Salinity Temperature	System[a]	Compound	Concentration (ppm)	Effect[b] (LC_{50}) (TLm)[c]	References
Morone saxatilis Striped bass Juveniles	25 ppt SW 16.0°C	Semi-Static	Benzene	6.9 5.8	24h[c] 96h[c]	Benville and Korn, 1977
			Toluene	7.3 7.3	24h[c] 96h[c]	
			Ethyl-benzene	4.3 4.3	24h[c] 96h[c]	
			p-Xylene	2.0 2.0	24h[c] 96h[c]	
			m-Xylene	9.2 9.2	24h[c] 96h[c]	
			o-Xylene	11.0 11.0	24h[c] 96h[c]	
Striped Bass Juveniles	29 ppt SW 17.4°C	Open Flow	Benzene	10.9	96h	Meyerhoff, 1975

Eleginus gracilis Saffron cod	26-30 ppt SW 3.7-11^{o}C	Semi-Static	WSF of Cook Inlet crude oil	2.48 2.28	24h^{c} 96h^{c}	Rice et al., 1976
			WSF of #2 fuel oil	>4.56 2.93	24h^{c} 96h^{c}	
Aulorhynchus flavidus Tube-snout	26-30 ppt SW 3.7-11^{o}C	Semi-Static	WSF of Cook Inlet crude oil	--- 1.34	24h^{c} 96h^{c}	Rice et al., 1976
			WSF of #2 fuel oil	--- ---	24h^{c} 96h^{c}	
Thymallus arcticus Arctic grayling	0 ppt FW 9^{o}C	Semi-Static	WSF of Prudhoe Bay crude oil	4.40	96h^{c}	Moles et al., 1979
	9^{o}C		Benzene	14.71	96h^{c}	
Cottus cognatus Slimy sculpin Juveniles	0 ppt FW 9^{o}C	Semi-Static	WSF of Prudhoe Bay crude oil	6.44	96h^{c}	Moles et al., 1979
	9^{o}C		Benzene	15.41	96h^{c}	
Gasterosteus aculeatus Three-spined stickleback Adults	0 ppt FW 5^{o}C	Semi-Static	WSF of Prudhoe Bay crude oil	>10.45	96h^{c}	Moles et al., 1979
	8^{o}C		Benzene	24.83	96h^{c}	

Table 11 con't.

Exposed Species/Stage	Salinity Temperature	System^a	Compound	Concentration (ppm)	Effect (LC$_{50}$)^b (TLm)^c	References
Lepomis macrochirus Bluegill Adults	0 ppt FW 25^{o}C	Static	Cyclohexane	42.33	24h^c	Pickering and Henderson, 1966
				40.00	48h^c	
				34.72	96h^c	
			Benzene	22.49	24h^c	
				22.49	48h^c	
				22.49	96h^c	
			Toluene	24.00	24h^c	
				24.00	48h^c	
				24.00	96h^c	
			Ethylbenzene	35.08	24h^c	
				32.00	48h^c	
				32.00	96h^c	
			Xylene	24.00	24h^c	
				24.00	48h^c	
				20.87	96h^c	
			Phenol	25.85	24h^c	
				23.88	48h^c	
				23.88	96h^c	
Carassius auratus Goldfish Adults	0 ppt FW 25^{o}C	Static	Cyclohexane	42.33	24h^c	Pickering and Henderson, 1966
				42.33	48h^c	
				42.33	96h^c	
			Benzene	34.42	24h^c	
				34.42	48h^c	
				34.42	96h^c	
			Toluene	57.68	24h^c	
				57.68	48h^c	
				57.68	96h^c	

			Ethylbenzene	94.44	24h[c]	
				94.44	48h[c]	
				94.44	96h[c]	
			Xylene	36.81	24h[c]	
				36.81	48h[c]	
				36.81	96h[c]	
			Phenol	49.86	24h[c]	
				49.13	48h[c]	
				44.49	96h[c]	
Poecilia reticulata Guppy 6 months old	0 ppt FW 25°C	Static	Cyclohexane	57.68	24h[c]	Pickering and Henderson, 1966
				57.68	48h[c]	
				57.68	96h[c]	
			Benzene	36.00	24h[c]	
				36.00	48h[c]	
				36.00	96h[c]	
			Toluene	62.81	24h[c]	
				60.95	48h[c]	
				59.30	96h[c]	
			Ethylbenzene	97.10	24h[c]	
				97.10	48h[c]	
				97.10	96h[c]	
			Xylene	34.73	24h[c]	
				34.73	48h[c]	
				34.73	96h[c]	
			Phenol	49.86	24h[c]	
				49.86	48h[c]	
				39.19	96h[c]	

Table 11 con't.

Exposed Species/Stage	Salinity Temperature	System^a	Compound	Concentration (ppm)	Effect^b (LC$_{50}$) (TLm)^c	References
Pimephales promelas Fathead minnow Adults	**0 ppt FW** Soft water 25^{o}C	Static	Cyclohexane	35.08	24h^c	Pickering and Henderson, 1966
				35.08	48h^c	
				32.71	96h^c	
			Benzene	35.56	24h^c	
				35.95	48h^c	
				33.47	96h^c	
			Toluene	46.31	24h^c	
				46.31	48h^c	
				34.27	96h^c	
			Ethylbenzene	48.51	24h^c	
				48.51	48h^c	
				48.51	96h^c	
			Xylene	28.77	24h^c	
				27.71	48h^c	
				26.70	96h^c	
			Phenol	40.60	24h^c	
				40.60	48h^c	
				34.27	96h^c	

Pimephales promelas Fathead minnow Adults	**0 ppt FW** Hard water 25^{o}C	Static	Cyclohexane	42.33	24h^c	Pickering and Henderson, 1966
				42.33	48h^c	
				42.33	96h^c	
			Benzene	34.42	24h^c	
				32.00	48h^c	
				32.00	96h^c	
			Toluene	56.00	24h^c	
				56.00	48h^c	
				42.33	96h^c	
			Ethylbenzene	42.33	24h^c	
				42.33	48h^c	
				42.33	96h^c	
			Xylene	28.77	24h^c	
				28.77	48h^c	
				28.77	96h^c	
			Phenol	38.62	24h^c	
				38.62	48h^c	
				32.00	96h^c	

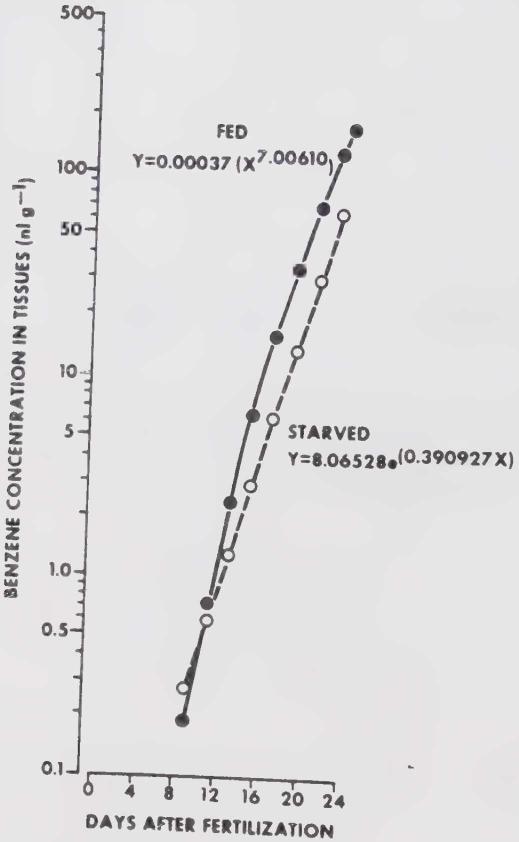


FIGURE 8. *Uptake and accumulation of ^{14}C-labeled benzene in feeding and starved larvae of the striped bass (Morone saxatilis), constantly exposed to a concentration of approximately 0.100 ppm ^{14}C-benzene through the water column (from Eldridge and Benville, ms in prep.).*

benzene to juveniles of different species are compared, salmonids appear slightly more sensitive than striped bass. Freshwater species such as the grayling, sculpin, stickleback, etc., appear less sensitive. The most sensitive to benzene was the sockeye salmon and the least sensitive, the guppy.

Among life history stages the most sensitive, at both acute and chronic levels, appears to be the feeding larvae, followed by gametes, prespawning adults, eggs, embryos and nonspawning adults. The least sensitive stage is the juvenile. This is in accord with the relative bioaccumulations at these stages (Table 9). Most acute bioassays are done with juvenile fish, although they appear to be the least sensitive to MAH. More susceptible stages should be selected for bioassays.

Recent work on striped bass (*Morone saxatilis*) and starry flounder (*Platichthys stellatus*) indicates that there may be intraspecific genotypic differences in the accumulation of MAH. This may mean that there is also intraspecific variability in susceptibility to the effects. In the striped bass, for example, intraspecific differences in color pattern and some meristic characteristics appear to correlate positively with the MAH concentration in liver and gonads (Whipple, 1979; Whipple *et al.*, ms in prep.). Factor analytic results are being examined for correlations between genotypic characters and concentrations of MAH (and other pollutants) in striped bass. Right- and left-eyed starry flounder also appear to vary in their relative uptake of MAH and other components in the WSF of Cook Inlet crude oil (Yocom *et al.*, ms in prep.). If laterality in starry flounder is genetically based, the variants may also differ physiologically and metabolically in their susceptibility to MAH.

Fish may also vary in sensitivity to MAH if they are already stressed by other environmental factors, or are low in energy reserves due to spawning or other stress (see Table 6). In striped bass, for example, there appears to be a strong relationship between poor condition (estimated by condition factors) and a higher concentration of MAH (Whipple, 1979; Whipple *et al.*, ms in prep.). The degree of parasitism (number of types, abundance, severity of host reactions) also appears to correlate with the tissue concentration of MAH (Whipple, 1979; Whipple *et al.*, ms in prep.). Cause and effect relationships, however, are as yet unclear. For example, does a heavily parasitized fish take up more MAH, or does a fish stressed by MAH also become more heavily parasitized, or do both events occur? Laboratory tests are planned to clarify this issue. Moles (1980) found that coho salmon fry (*Oncorhynchus kisutch*), infested with clam glochidia of *Anodonta oregonensis* were significantly more sensitive to toluene, naphthalene and the WSF of Prudhoe Bay crude oil than uninfested fish.

Work is also being done to measure the pollutant load in striped bass from San Francisco Bay, including not only MAH, but heavy metals, PCB's, pesticides, etc. (Whipple, 1979, 1980; Whipple *et al.*, 1979; Whipple *et al.*, ms in prep.). This work is still underway; however, results so far show high loads of zinc, copper, mercury, PCB's and others (Jung and Bowes, 1980). The interaction of the existing pollutant load with MAH uptake in striped bass is being studied.

The relative toxicity of individual monocyclics (Table 11) varies with their solubility and bioaccumulation. The position of the alkyl substitution on the aromatic ring also appears to affect toxicity (Benville and Korn, 1977). In general, *p*-xylene and benzene appear most toxic to fish, while toluene, *m*- and *o*-xylene are least toxic. Ethylbenzene is usually intermediate in toxicity. In comparison, cyclohexane and phenol (phenol is a major metabolite of monocyclics) are about as toxic as toluene (Pickering and Henderson, 1966; Table 11).

Exposure periods in most acute bioassays (Table 11) are 24, 48 and 96 hrs. For most MAH the toxicity at 24 hrs does not vary significantly from that at 96 hrs. We have found that, although death may not occur at selected exposure levels, delayed mortality often occurs after 96 hrs (Struhsaker *et al.*, 1974). We feel that it is important to examine surviving fish for some time after termination of exposure. The length of exposure relative to MAH concentration is very important and should be considered in tests of the effects of MAH on fishes, particularly when interested in chronic low level effects, such as may occur in a polluted estuary.

The source of exposure in most acute bioassays is through the water column only. As discussed above, there appears to be little accumulation through food and thus toxic effects would not be expected through this route.

Studies done at Auke Bay, Alaska (Rice *et al.*, 1976; Moles *et al.*, 1979) showed that temperature and salinity affect the toxicity of MAH and the WSF of crude oil (Table 11). MAH are usually more toxic to fish in seawater than in freshwater, and more toxic at lower temperatures. Freshwater fish also appear to be slightly more sensitive to some MAH in hard water (higher alkalinity) than in soft water (Pickering and Henderson, 1966; Table 11).

The interaction of the MAH with one another, with other hydrocarbons in the WSF of crude oil, and with other classes of pollutants (such as chlorinated hydrocarbons and heavy metals) is obviously complex. Little is known about whether effects are additive, synergistic or antagonistic (Caldwell *et al.*, 1977). An acute bioassay of benzene and the WSF of Prudhoe Bay crude oil on salmonids (Table 11) shows that the toxicity of the WSF is greater than that of benzene alone. Generally in acute bioassays, the polycyclic aromatics appear to be more toxic and more persistent in tissues than the MAH (Rice *et al.*, 1977; Neff, 1979). However, in the environment their solubility in water is much less and the uptake probably lower. Field data from San Francisco Bay also indicate that dicyclics are not being bioaccumulated in striped bass (Tables 4 and 5). Alkyl cyclohexanes may be an important chronic pollutant interacting with MAH, since they are bioaccumulated to a higher degree and are more persistent (Tables 4, 5 and 8) and methylcyclohexane is about as toxic as toluene (Table 11). Competitive inhibition or stimulation between chlorinated hydrocarbons and petroleum hydrocarbons is probable, depending upon relative levels and their demand on the MFO system for detoxification (LaDu *et al.*, 1971). Heavy metals often act as inhibitors of the enzymes in the MFO system and could potentiate the effects of hydrocarbons, including monocyclics, by decreasing the rate of metabolic detoxification and increasing accumulated levels in target organs (Maines and Kappas, 1977). Further studies on the interactions of components within these major classes of pollutants are badly needed before we can determine their combined effects on fishes in the environment.

Hypothesized Modes of Action

We still know very little about the modes of action of MAH or other petrochemicals. We know that effects of MAH will differ according to several factors discussed previously, among them: 1) the life history, 2) the exposure level (lethal, high or low sublethal) and 3) the length of the exposure (short-term acute vs. long-term chronic). Similar effects probably occur whether fish are exposed to MAH, other aromatics (e.g., PAH), the total WSF of crude oils, or even other classes of hydrocarbons. Effects specifically attributable to single compounds are rare, or at least difficult to ascertain. From the literature it appears that effects of exposure to chlorinated hydrocarbons (pesticides) are similar to those observed in fishes exposed to petroleum hydrocarbons. A possible explanation is that the modes of action of most toxic hydrocarbons are similar, and that many effects are a result of a generalized enzymatic and hormone-mediated syndrome of responses to stress, similar no matter what the stressor. We hypothesize that four effect syndromes are generally seen: 1) effects due to inhibition or stimulation of enzymatic systems in metabolism, 2) hormone-mediated adaptive responses, 3) damage to organs due to hormone-mediated responses and 4) damage due to specific effects of an individual compound. Which responses occur probably depends primarily on the concentration and length of the exposure.

The hypothesized modes of action and effects are summarized in Table 12. Several of these modes of action are still hypothetical, and are meant to act only as temporary guidelines for study of the effects of MAH on fishes. Where observations or research tend to substantiate these hypotheses, references are noted.

Table 12. Some hypothesized modes of action and effects (functional and structural) of monocyclic aromatic hydrocarbons (MAH) at different life history stages and at different concentration levels of exposure. Hypothetical relationships are indicated by an asterisk.

	LOW SUBLETHAL EXPOSURES OF MAH			
	Early Life History Stages (Ref. Nos. 2, 11, 19-23, 49, 55, 77, 82, 92-94)			
Organizational Level of Effect: (Effects often delayed)	Spawned eggs, embryos to newly hatched larvae		Feeding larvae	
Cellular	*Stimulation of metabolism *Increased ATP, enzyme activity *Accelerated cellular respiration *Increased oxygen requirement			
Tissue and/or Organ System	Energy allocation altered		Energy allocation altered	
	Yolk-oil energy diverted to compensate for toxicant effect	Less yolk and/or oil	Remaining yolk-oil rapidly utilized	
	Accelerated heartbeat, development rate; increased respiration		Accelerated development rate; increased respiration	Accelerated organogenesis
Individual	Premature hatching; smaller, less viable larvae	Less buoyant or active larvae	Smaller larvae, less active	
Population	Decreased growth, survival		Desynchronization of first feeding	Decreased growth, survival

HIGH SUBLETHAL EXPOSURES OF MAH

Early Life History Stages
(Ref. Nos. 19-23, 49, 55, 77, 82, 88, 92-94)

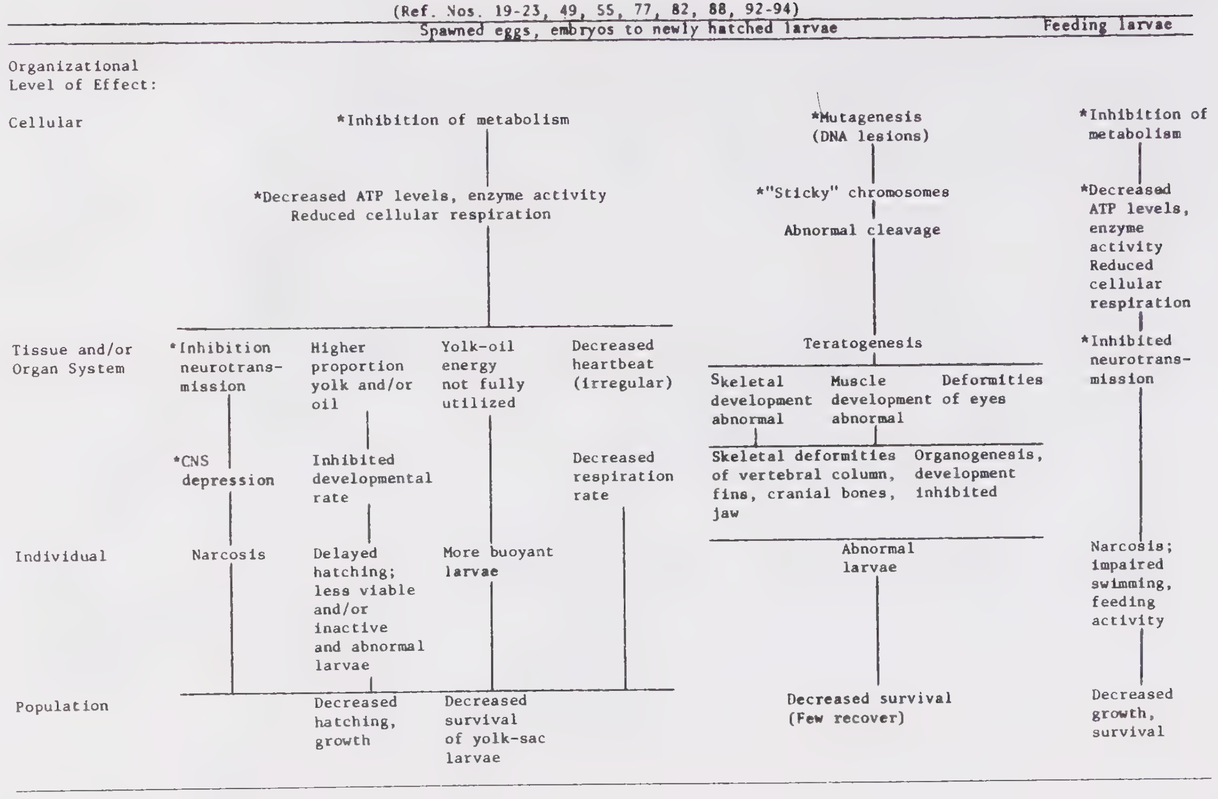
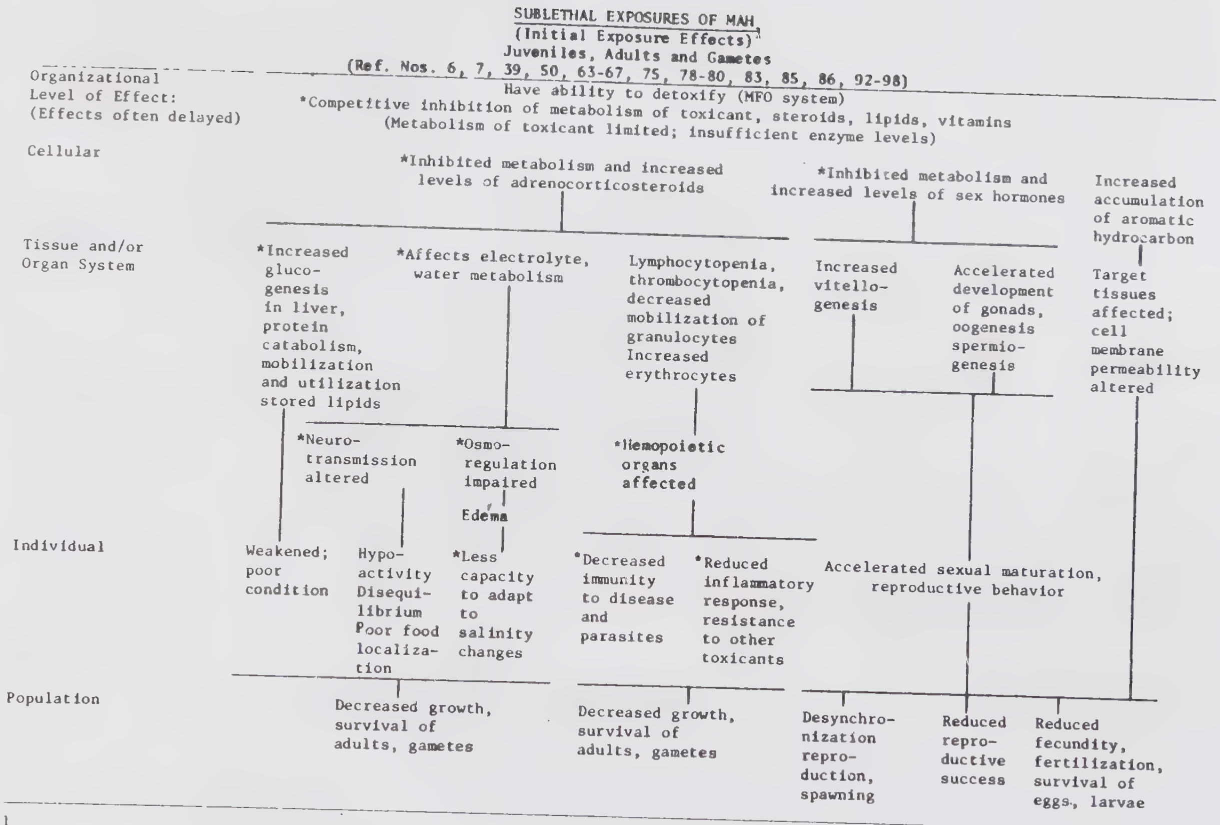

Spawned eggs, embryos to newly hatched larvae
Feeding larvae
Organizational Level of Effect:
Cellular
Tissue and/or Organ System
Individual
Population
*Inhibition of metabolism
*Decreased ATP levels, enzyme activity Reduced cellular respiration
*Inhibition neurotrans-mission
Higher proportion yolk and/or oil
Yolk-oil energy not fully utilized
Decreased heartbeat (irregular)
*CNS depression
Inhibited developmental rate
Decreased respiration rate
Narcosis
Delayed hatching; less viable and/or inactive and abnormal larvae
More buoyant larvae
Decreased hatching, growth
Decreased survival of yolk-sac larvae
*Mutagenesis (DNA lesions)
*"Sticky" chromosomes
Abnormal cleavage
Teratogenesis
Skeletal development abnormal
Muscle development abnormal
Deformities of eyes
Skeletal deformities of vertebral column, fins, cranial bones, jaw
Organogenesis, development inhibited
Abnormal larvae
Decreased survival (Few recover)
*Inhibition of metabolism
*Decreased ATP levels, enzyme activity Reduced cellular respiration
*Inhibited neurotrans-mission
Narcosis; impaired swimming, feeding activity
Decreased growth, survival

Table 12 con't.


SUBLETHAL EXPOSURES OF MAH
(Initial Exposure Effects)[1]
Juveniles, Adults and Gametes
(Ref. Nos. 6, 7, 39, 50, 63-67, 75, 78-80, 83, 85, 86, 92-98)
Organizational Level of Effect: (Effects often delayed)
Have ability to detoxify (MFO system)
*Competitive inhibition of metabolism of toxicant, steroids, lipids, vitamins
(Metabolism of toxicant limited; insufficient enzyme levels)
Cellular
*Inhibited metabolism and increased levels of adrenocorticosteroids
*Inhibited metabolism and increased levels of sex hormones
Increased accumulation of aromatic hydrocarbon
Tissue and/or Organ System
*Increased gluco-genesis in liver, protein catabolism, mobilization and utilization stored lipids
*Affects electrolyte, water metabolism
Lymphocytopenia, thrombocytopenia, decreased mobilization of granulocytes Increased erythrocytes
Increased vitello-genesis
Accelerated development of gonads, oogenesis spermio-genesis
Target tissues affected; cell membrane permeability altered
*Neuro-transmission altered
*Osmo-regulation impaired
Edema
*Hemopoietic organs affected
Individual
Weakened; poor condition
Hypo-activity Disequi-librium Poor food localiza-tion
*Less capacity to adapt to salinity changes
*Decreased immunity to disease and parasites
*Reduced inflammatory response, resistance to other toxicants
Accelerated sexual maturation, reproductive behavior
Population
Decreased growth, survival of adults, gametes
Decreased growth, survival of adults, gametes
Desynchro-nization repro-duction, spawning
Reduced repro-ductive success
Reduced fecundity, fertilization, survival of eggs, larvae

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[1] Also effects if homeostasis fails and negative feedback occurs.

SUBLETHAL EXPOSURES OF MAH
(Adaptation to Exposure)
Juveniles, Adults and Gametes
(Ref. Nos. 6, 7, 39, 50, 63-67, 75, 78-81, 83, 85, 86, 92-98)

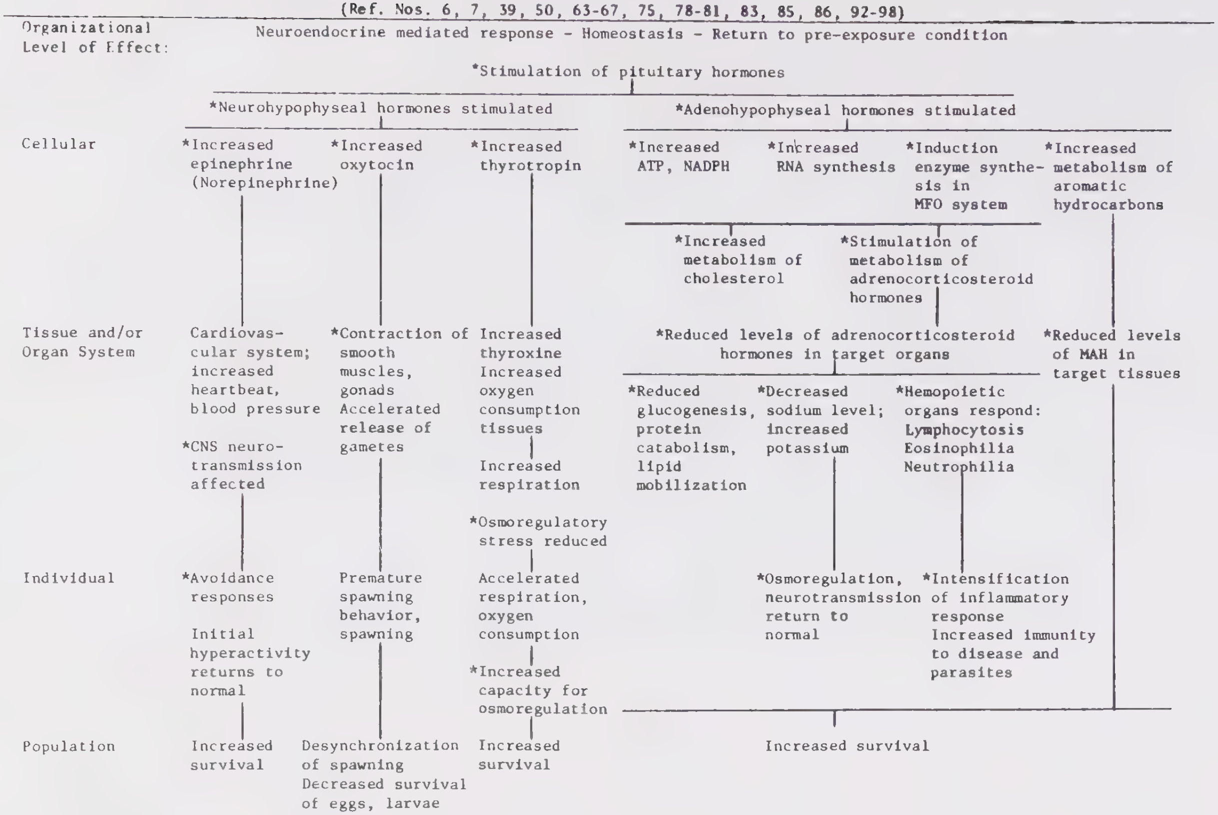

Organizational Level of Effect:
Neuroendocrine mediated response - Homeostasis - Return to pre-exposure condition
*Stimulation of pituitary hormones
*Neurohypophyseal hormones stimulated
*Adenohypophyseal hormones stimulated
Cellular
*Increased epinephrine (Norepinephrine)
*Increased oxytocin
*Increased thyrotropin
*Increased ATP, NADPH
*Increased RNA synthesis
*Induction enzyme synthesis in MFO system
*Increased metabolism of aromatic hydrocarbons
*Increased metabolism of cholesterol
*Stimulation of metabolism of adrenocorticosteroid hormones
Tissue and/or Organ System
Cardiovascular system; increased heartbeat, blood pressure
*CNS neurotransmission affected
*Contraction of smooth muscles, gonads
Accelerated release of gametes
Increased thyroxine
Increased oxygen consumption tissues
Increased respiration
*Osmoregulatory stress reduced
*Reduced levels of adrenocorticosteroid hormones in target organs
*Reduced levels of MAH in target tissues
*Reduced glucogenesis, protein catabolism, lipid mobilization
*Decreased sodium level; increased potassium
*Hemopoietic organs respond: Lymphocytosis Eosinophilia Neutrophilia
Individual
*Avoidance responses
Initial hyperactivity returns to normal
Premature spawning behavior, spawning
Accelerated respiration, oxygen consumption
*Increased capacity for osmoregulation
*Osmoregulation, neurotransmission return to normal
*Intensification of inflammatory response
Increased immunity to disease and parasites
Population
Increased survival
Desynchronization of spawning
Decreased survival of eggs, larvae
Increased survival
Increased survival

Table 12 con't.

LOW SUBLETHAL EXPOSURES OF MAH
(Negative feedback over longer chronic exposure)
Juveniles, Adults and Gametes
(Ref. Nos. 7, 39, 81, 92-97, 101)

Organizational Level of Effect:	*Increased competition for energy (ATP) required for metabolism and/or detoxification			
Cellular	*Decreased energy available for anabolism, respiration			*Decreased metabolism of MAH
Tissue and/or Organ System	Decreased vitellogenesis Atresia of eggs	*Decreased lipid mobilization to liver	*Decreased muscle tissue, stored lipids, liver glycogen	*Increased levels of MAH in target tissues
	Reduced size, resorption of gonads	Reduced size of tissues, organs		Reversible and irreversible effects on target tissues
Individual	Inhibition of maturation, reproduction	Reduced growth, activity and capacity to respond to additional stress, e.g., disease, parasites		
		Poor condition		
Population	Reduced reproductive success, fecundity	Reduced growth (biomass)	*Reduced survival or life span	*Reduced survival or life span

SUBLETHAL EXPOSURES OF MAH

Toxic effects on target tissues possibly resulting from hormone-mediated, adaptive responses; chronic exposure (Ref. Nos. 6, 7, 39, 50, 63-67, 75, 78-81, 86, 92-98)

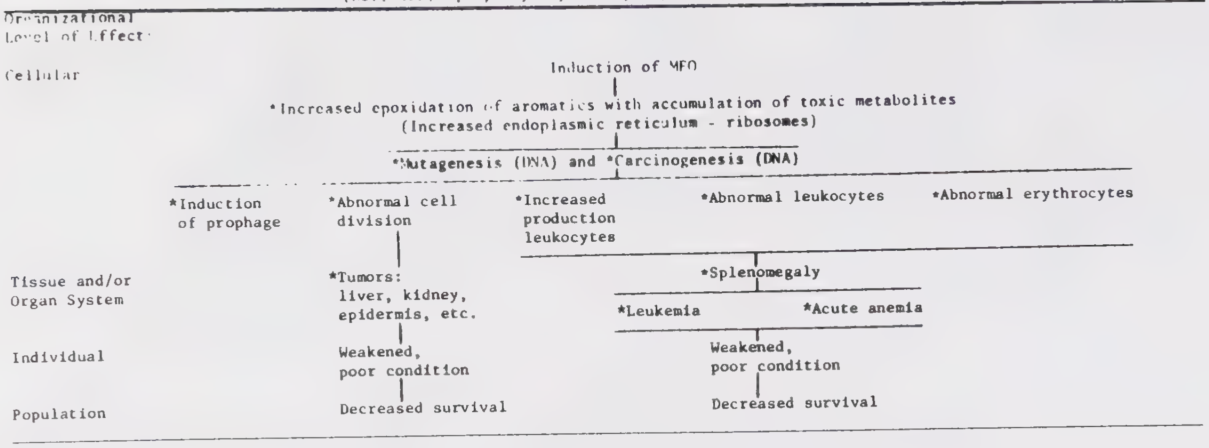
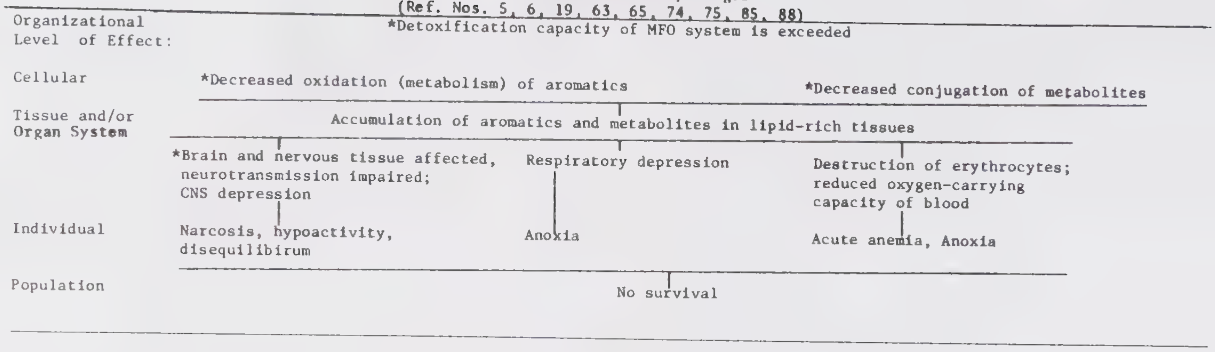

Organizational Level of Effect:
Cellular
Induction of MFO
*Increased epoxidation of aromatics with accumulation of toxic metabolites (Increased endoplasmic reticulum - ribosomes)
*Mutagenesis (DNA) and *Carcinogenesis (DNA)
*Induction of prophage
*Abnormal cell division
*Increased production leukocytes
*Abnormal leukocytes
*Abnormal erythrocytes
Tissue and/or Organ System
*Tumors: liver, kidney, epidermis, etc.
*Splenomegaly
*Leukemia
*Acute anemia
Individual
Weakened, poor condition
Weakened, poor condition
Population
Decreased survival
Decreased survival

Table 12 con't.

SUBLETHAL AND LETHAL EXPOSURES OF MAH
(Some toxic effects on target tissues resulting from increased levels of MAH and/or metabolites)
Most life history stages
(Ref. Nos. 4-7, 19-24, 39, 49, 50, 63-67, 74, 75, 77-81, 86-88, 92-98, 101)

Organizational Level of Effect: (Effects often delayed)	Detoxification capacity of MFO exceeded and/or toxic metabolites not depurated				
	Accumulation of aromatics and/or metabolites in target tissues and organs				
Tissue and/or Organ System	Liver: Lipid deposition *Change in type of lipid *Glycogen depletion Disruption of hepatic muralia Fibrotic infiltration Hypertrophy Hemorrhage; sinusoidal congestion with erythrocytes Necrosis	Ovaries: Increased vitellin in eggs, or atresia-resorption Egg membranes disrupted Egg vacuolization Reduced blood supply to eggs Erythrocyte destruction Hemorrhage Necrotic foci Testes: Resorption Hemorrhage Necrotic foci *Reduced sperm motility	Spleen: *Hypoplasia or *Hyperplasia Fibrotic infiltration Granulomas Blood: Abnormal erythrocytes, leukocytes Destruction erythrocytes *Increased erythrocyte fragility *Cell membrane disruption *Increased lipoprotein	Heart: *Fatty infiltration Blood Vessels: Sloughing of endothelial lining *Vasodilation *Increased capillary permeability Gills: Increased mucus secretion Increased number mucus cells Lesions, vacuoles Epithelial sloughing	Brain & Nerve Tissue: *Lesions in hypothalamus, pituitary, optic nerve tract, olfactory bulbs Adrenals: Enlarged size Muscle: *Decrease in muscle tissue, less lipid; edema
Individual	Decreased metabolic efficiency Poor condition	Decreased reproduction	Decreased respiration, immunity, resistance to environmental extremes	Decreased cardiovascular efficiency Decreased respiratory efficiency and osmoregulation	Impaired neurotransmission and behavioral responses Neuroendocrine stress responses Reduced activity
Population	Decreased growth, survival	Decreased fecundity Reduced fertilization and reproductive success	Decreased growth, survival	Decreased growth, survival	Decreased growth, survival

LETHAL EXPOSURES OF MAH
All life history stages
(Ref. Nos. 5, 6, 19, 63, 65, 74, 75, 85, 88)


Organizational Level of Effect:
*Detoxification capacity of MFO system is exceeded
Cellular
*Decreased oxidation (metabolism) of aromatics
*Decreased conjugation of metabolites
Tissue and/or Organ System
Accumulation of aromatics and metabolites in lipid-rich tissues
*Brain and nervous tissue affected, neurotransmission impaired; CNS depression
Respiratory depression
Destruction of erythrocytes; reduced oxygen-carrying capacity of blood
Individual
Narcosis, hypoactivity, disequilibirum
Anoxia
Acute anemia, Anoxia
Population
No survival

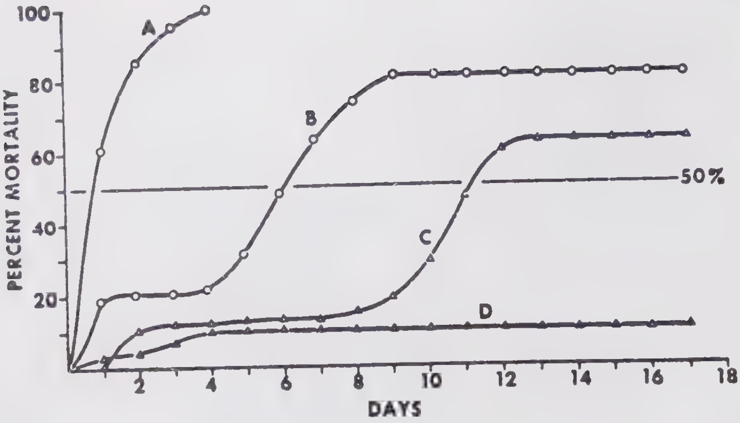


*FIGURE 9. Mortality curves of anchovies (*Stolephorus purpureus*) exposed to different levels of osmoregulatory stress in the laboratory. A = lethal (or acute) stress; B and C = High sublethal (eventually lethal) stress; D = Low sublethal (chronic) stress (Adapted from Struhsaker* et al., *1974).*

To illustrate the responses of fish to stress, Figure 9 shows a family of mortality curves generated by exposing anchovies to osmoregulatory stress (Struhsaker *et al.*, 1975). The percent mortality over a 17-day period is shown at different levels of stress (from lethal to low sublethal). The configuration of two of these curves (B and C) is similar to the general adaptation syndrome (GAS) described by Selye (1950) (see also Rosenthal and Alderdice, 1976). A lethal level of stress is represented by curve A, where continuous mortality occurs until 100% of the fish are dead. At this level, no homeostatic or adaptive response was adequate to overcome the effects of the stress. In curves B and C, there was an initial mortality, followed by an adaptive response with zero mortality, followed by a negative feedback where capacity to adapt was exceeded and mortality again increased. Finally, mortality leveled off with some of the fish surviving. The survivors probably represent a genetically resistant portion of the population with greater adaptive capacity. Curve D is equivalent to what may occur with low sublethal exposures, where there may be a small initial mortality (or none) followed by an adaptive response of long duration. Ultimately, however, negative feedback may occur. There is disagreement among researchers as to whether there is a threshold level of "no effect" for many pollutants.

Some believe that there is no "safe level" of exposure if organisms are exposed to pollutant stress for a sufficiently long period of time. For example, the negative feedback may shorten the life span, decrease growth or inhibit reproduction. This issue has not been resolved at the present time.

Chronic Effects

Many of the observed effects of MAH are probably due to a generalized stress response. A possible specific toxic effect may occur with the component benzene. In mammals, benzene affects the blood-forming organs, resulting in leukemia. This effect was observed to be specific to benzene and was not induced by other aromatic compounds (Gerarde, 1960). Preliminary studies of field-captured striped bass indicate that there are effects on red and white blood cells which are correlated with high levels of benzene in the liver (Whipple, 1979). Further studies on hemopoietic tissues are being done. The degree of a toxic effect will depend largely on the levels of the monocyclics and/or metabolites, such as phenol, in the target tissues. Our research has also shown that prespawning females, their ovaries, eggs and larvae experience irreversible damage to tissues at very low levels of MAH in the water column (50-100 ppb) and thus are potentially the most sensitive in the actual environment (Struhsaker, 1977; Whipple *et al.*, 1978b).

Several other effects are shown in Table 12. Many of the hypothesized modes of action and effects have been derived from work on mammals (summarized by LaDu *et al.*, 1971). In the table, hypothetical concepts are indicated by asterisks, while those with studies substantiating the hypotheses are referenced by numbers.

Many researchers have noted an apparent beneficial effect of exposure of fishes to low levels of toxicants, including the MAH (Eldridge *et al.*, 1977). This probably results from the hormone-mediated adaptive responses of the organisms to stress, at least temporarily stimulating metabolic functions. This response is referred to by Smyth (1967) as a "sufficient challenge". Under chronic conditions, however, we feel that some negative feedback eventually occurs (Table 12).

Hypothesized Effects at the Population Level

The effects of monocyclics summarized in Table 12 include potential effects at a population level. In essence, these effects may result in the reduction in production of a fishery as determined by fecundity, reproduction and larval recruitment, growth and survival. For example, our work has shown that such effects of MAH are possibly contributing to the decline of the striped bass population and fishery in the San Francisco Bay area (Whipple, 1979, 1980; Whipple *et al.*, ms in prep.). Chronic levels of MAH occur in tissues of striped bass which either alone, or in concert with other pollutants identified (e.g., zinc), are sufficient to cause negative effects. Although striped bass are relatively hardy, many appear to be stressed beyond their capacity to adapt. We hypothesize monocyclic aromatic petrochemicals reduce the ability of fishes to adapt to natural stresses, particularly during spawning migration and early life history stages. Whether or not a population can genetically adapt to this stress over longer periods depends upon the differential selection of a hardier genotype. Although such intraspecific diversity appears to exist in striped bass, present observations indicate that it is not sufficient to ensure population persistence.

Estimates of reduction in fecundity and larval survival due to the uptake of monocyclic aromatics (both laboratory and field data) indicate that a reduction of larval recruitment as high as 40-50% may occur in some of the species studied, for example, Pacific herring and striped bass (Struhsaker, 1977; Whipple *et al.*, ms in prep.) at the chronic levels now occurring in San Francisco Bay.

SUMMARY

Recent investigations of the sources of monocyclic aromatic hydrocarbons (MAH) and their potential effects on aquatic resources indicate that this hydrocarbon class is prevalent in estuarine ecosystems such as the San Francisco Bay-Delta, and may constitute a chronic pollution threat. These toxic petrochemicals, interacting with other pollutants, could cause quantitative reductions in the production of fish populations by decreasing growth, reproduction, egg viability, larval recruitment and survival. There are also qualitative effects on fisheries, such as condition of fish flesh and increased parasitism and disease. This paper briefly discusses the sources and fates of MAH and summarizes their effects on fishes.

The chronic effects of monoaromatics are examined in the context of a qualitative conceptual model, suggesting interactive effects of inherent environmental factors (abiotic and biotic). Variability in uptake, bioaccumulation and

effects of monocyclics is considered in relation to inherent differences in fishes (e.g., interspecies variation, intraspecific variation in genotype, sex, age or life history stage and condition). The interaction of these inherent differences with certain environmental variables (e.g., temperature, salinity, pollutants and parasitism) is also discussed. The definition of variability is important in determining potential chronic effects on the biota, and in making selections of critical stages and effects to study and monitor.

Monocyclic aromatics discussed include: benzene, toluene, xylenes, ethylbenzene and substituted benzenes, in general. Examples of fish species are drawn from our research in the San Francisco Bay-Delta area. However, most of these species are widely distributed into other areas. Species discussed include: striped bass (*Morone saxatilis*), starry flounder (*Platichthys stellatus*), Pacific herring (*Clupea harengus pallasii*), northern anchovy (*Engraulis mordax*) and Chinook salmon (*Oncorhynchus tshawytscha*). The possible relationship of selected genotypic differences to variability in uptake, bioaccumulation and effects is discussed for striped bass and starry flounder. Differences among the following life history stages also occur: spawning adults, gametic eggs, spawned eggs, embryos, larvae, juveniles and nonspawning adults. Larvae, for example, appear to bioaccumulate very high levels of monocyclic aromatics.

Uptake, bioaccumulation, translocation and depuration of these components are discussed in relation to effects in terms of hypothesized modes of action and alterations of structure and function (morphology, physiology and behavior). Many responses appear to be nonspecific responses to pollutant stress, but some specific effects (e.g., blood parameters) may also occur.

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THE EFFECT OF INHERENT PARENTAL FACTORS ON GAMETE CONDITION AND VIABILITY IN STRIPED BASS (*MORONE SAXATILIS*)

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One hundred years ago (1879), 332 juvenile striped bass from the Navesink River on the east coast of the United States were released into the San Francisco Bay-Delta estuary of California in a successful introduction of an east coast species to the Pacific.

Over the intervening years, sport and commercial catch records have indicated considerable fluctuations in the Pacific striped bass population (Smith and Kato, in press). To determine the causal mechanisms controlling these fluctuations, California Department of Fish and Game (CDF&G) has conducted extensive studies since 1958 on the California striped bass and their habitat.

CDF&G field data indicate that mortality during the first 60 days after hatching determines the size of the adult population. Abundance of young-of-the-year juveniles is related to river outflows and diversion volumes in the Sacramento-San Joaquin River Delta (Chadwick et al., 1977).

However, aside from direct export of eggs and larvae out of the estuary via water diversions, the primary causes of mortality remain undetermined. There is no clear understanding of the primary mortality factors determining survival of striped bass during the first two months of life. In 1976 the NMFS Tiburon Laboratory in an effort to improve abundance forecasts of striped bass recruitment began intensive laboratory studies on mortality factors affecting egg and larval stages of striped bass (Eldridge et al., 1977; Eldridge et al., 1978). Studies were also initiated on the effects of selected inherent factors such as the condition of spawning adults and their genotypes on gametic viability of eggs. Our previous research on effects of aromatic petroleum hydrocarbons showed that fish during spawning condition were extremely sensitive to short, low-level exposures (Struhsaker, 1977; Whipple et al., 1978). There were also subsequent deleterious effects on survival and growth of eggs and larvae from exposed females.

In the spring of 1978, samples of adult striped bass were collected off Antioch, California on the San Joaquin River during their upstream spawning migration and after they passed through the heavily industrialized Carquinez Straits area. Post-spawning adults were collected in San Francisco Bay near the Tiburon Laboratory.

A total of 73 migrating, pre-spawning and 100 post-spawning individuals were collected, and 165 parameters were measured for each fish. Complete autopsies were performed and subsamples taken for various measurements. The purpose of this sampling was: (1) to determine the condition of parental fish just prior to spawning and to ascertain whether certain measures of parental condition correlated with measures of gametic viability, and (2) to identify factors which might relate to the annual "fish kill" of adult striped bass in the Carquinez Straits during the summer.

We have obtained results which indicate that pre-spawning fish, their gonads and gametes, and post-spawning fish are being deleteriously affected during their migration through the San Francisco Bay-Delta estuary, and that the degree of this effect is determined by interaction of the parental genotype with environmental stress factors, including pollutants. Factor analysis of 165 variables (22 data sets, Table 1) and covariance analyses of factors were performed.

Table 1. Striped bass field samples (1978): data sets collected. (Total of 165 variables measured).

1. Field sampling — environmental and capture data
2. Meristics; length, width, age, etc.
3. Color pattern
4. Gonads; length, width, weight, fecundity
5. Liver, gall bladder, stomach
6. Parasites and disease
7. Histology — gonads
8. Histology — other — liver, spleen, kidney, etc.
9. Chemistry — lipids, carbohydrates, proteins, calorimetry
10. Chemistry — iron and heavy metals
11. Chemistry — pigments
12. Pollutants — petroleum aromatic hydrocarbons, aryl cyclohexanes
13. Pollutants — pesticides — chlorinated hydrocarbons, PCBs
14. Pollutants — other pollutants
15. Electrophoresis — total protein, TFN, albumin
16. Blood — hemoglobin, hematocrit, erythrocyte fragility
17. Blood cells — red blood cells

18-21. Blood cells — white blood cells; thrombocytes, lymphocytes, monocytes, macrophages, granulocytes, neutrophils, eosinophils, basophils

22. Egg diameters

In summary, the results show there is genotypic variability in the serum proteins albumin and transferrin, the egg pigments (varying shades of green to yellow), melanistic color patterns, and certain meristic characters. The variability in some of these characteristics correlates with different physiological types, varying in their resistance to environmental exigencies and parasitism.

A high percentage of the parental fish were in poor condition, as indicated by body condition factors (low), macroscopic observations during autopsy, body lesions (approx. 35%), level of parasitism (approx. 50% showing parasitic damage to organs), and the blood cells (low numbers of lymphocytes, high numbers of granulocytes), among other parameters. Liver and ovarian tissues sampled were found to contain high levels of zinc (up to 90 ppm; wet weight) and aromatic and aryl cyclohexane petroleum hydrocarbons (up to 2 ppm; wet weight). There was a correlation between the poor condition of parental fish and the ability to reproduce (12% of adult females did not ripen, 20% of those ripening had damaged ovaries, parasitism, or dead eggs in ovaries). Fecundity and viability of eggs was reduced in the adults in poorer condition and/or with high pollutant content.

The overall decline in the striped bass population may be partially attributable to decreased reproduction and fecundity due to increasing effects of pollution, interacting with diversion and the low outflow years to increase mortality. Some mortality in the adult population also occurs, possibly because the adults are highly stressed from the interaction of pollutant and parasitic stress with spawning stress. The adults experience further stress as they migrate downstream through Carquinez Straits after spawning, encountering salinity and pollution stresses in the null zone, and a proportion of "weaker" fish die. The interaction of these factors may explain the annual "fish kills" in early summer (Kohlhorst, 1973). Further studies are being conducted.

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ESTIMATES OF ABUNDANCE AND MORTALITY OF LARVAL ANCHOVIES (1951–75): APPLICATION OF A NEW METHOD

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A method for analysis of egg and larval survey data based upon the maximum likelihood solution for the parameters of a modified negative binomial frequency model for the observed counts is described. The effect of uncontrollable variations in the real or "effective sampler size" and size-dependent levels of aggregation are incorporated as a fundamental part of the estimation procedure. Using this model, we calculated regional-seasonal estimates of abundance and mortality of northern anchovy larvae, *Engraulis mordax*, for the years 1951–75.

As a result of these analyses, we conclude that estimates of average catch, mortality and confidence intervals based upon semi-log regressions of the logarithm of the average standardized catch (rather than the logarithms of the individual observations) with time or age do not differ greatly from the estimates based upon the complete maximum likelihood solutions. Estimates of mean abundance and mortality generally coincided with estimates of the strength of a year-class obtained from fishery data. However, we were unable to consistently detect changes in recruitment using the parameters chosen for this study.

Equations are given for estimating the intensity of sampling required for a desired degree of precision in the relative coefficient of variation $s_{\bar{x}} / \bar{x}$. The methods described herein may be used for more sophisticated kinds of analyses to: (1) uncover hitherto unrecognized relationships among abundance, aggregation, coverage and mortality which may be indicative of changes in absolute or relative levels of recruitment; and (2) determine the most efficient allocation of effort in the field and laboratory.

INTRODUCTION

Fishery management of short-lived stocks requires frequent estimates of spawning stock size; in addition, short-lived pelagic stocks may require estimates of recruitment. For example, northern anchovy, *Engraulis mordax*, that were prespawners in autumn 1974 comprised only 13% by numbers of the catch in the 1975 season while 90% of the 1959 catch were prespawners in the winter of 1958. Young-of-the-year (0-group) anchovies vary from 1 to 70% of the catch by number. This variation in recruitment to the fishery warrants full life-cycle monitoring for predictive purposes.

It has been shown that egg and larval surveys can be used effectively to monitor relative changes in spawning biomass (Smith, 1972). However, the value of such data for direct estimates of the abundance of the mature or exploited stock and/or recruitment has yet to be demonstrated. Direct estimates of abundance require, at a minimum, accurate determinations of egg production; and estimates of recruitment require, in addition to egg production estimates, reliable estimates of mortality. Even then, the stock size-recruitment relationship is complex. Recruitment to the stock may be due to areally-or temporally-protracted spawning or to higher than average survival at any prerecruitment stage either inside or outside the population center. Potentially reliable indexes of recruitment strength may consist of estimates of abundance at any or all early life stages, and/or estimates of mortality over restricted or extensive size ranges, and estimates of the extent of the area of spawning.

The conceptual models for estimates of stock abundance from the spawning products have been formulated (e.g., Saville, 1964). But the sampling or statistical considerations which, at least for large scale surveys, are primal have received little attention. English (1964) noted that the usefulness of several proposed indexes was severely limited by the lack of knowledge concerning their inherent variability. For statistical reliability, large scale surveys should consider:

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1) the effect of environmental and behavioral factors on the content of the samples or collections;
2) the effect of environmental and behavioral factors on the disposition of the population being sampled; and,
3) the temporal-areal allocation of sampling.

The first consideration is central to this paper and concerns the accuracy and precision of stock size and recruitment indexes for the population actually sampled. We attempt to remove the biases and variability due to change in catchability from bias and variability due to the disposition of organisms in the environment. The latter two issues concern the accuracy and precision with which these indexes monitor the total population and can be assessed only in relation to the allocation of sampling and the analysis technique. We use "catchability" in a somewhat restricted sense to represent the probability of capture within the area actually sampled. In the more general interpretation, catchability may include, in addition, the probability of being within the sampling area.

Based on the assumption of a completely effective sampler and using logarithmic transformation of the numbers of fish eggs, English (1964) used the analysis of variance to separate the temporal-spatial (both horizontal and vertical) components of variance and their interactions. He rejected indexes of stock size based on estimates of abundance during short periods or those relying on a few locations over the spawning period because of the complex fluctuations in spawning activity and because of the lack of confidence limits to accompany such indexes. In part to examine this complexity in larval fish, we calculated a series of regional-seasonal estimates of abundance and mortality of anchovy larvae for the years 1951–75. This series was also intended for comparison with other environmental and biological information (see Smith et al., this volume) and to explore the general applicability of the analysis technique. We use the data from one region [(7) Fig. 1] and season (Jan–Mar) of 1969 in the examples of the methods of analysis.

The analyses are based on the negative binomial weighted (NBW) model described by Bissell (1972a) for situations in which the actual size of the sample element was not constant. In his formulation, a weight w_i is used to define the total likelihood of N collections (e.g., counts of larvae) x_i in terms of the probabilities

$$\underset{..}{L} = \prod_{i=1}^{N} \Pr(x_i|m,k,w_i) = \prod_{i=1}^{N} \left(\frac{k}{mw_i+k}\right)^k \left(\frac{mw_i}{mw_i+k}\right)^{x_i} \frac{\Gamma(k+x)}{\Gamma(x+1)\Gamma(k)}$$

where $E(x_i)=mw_i$ and $Var(x_i) = mw_i(1 + mw_i/k)$. The resultant parameter estimates m and k are appropriate for the case $w = 1$.

We generalize the application of this model to situations where the sample elements vary in actual as well as "effective" size, i.e., where catchability is influenced by known physical and environmental factors. In our model, the weight w_i which corresponds to the catch x_i represents the "effective sampler size" and is determined by the larval size and by conditions local to the area of collection. In this way sample frequencies which are, in reality, an amalgam of observations determined by the vagaries of sampling may be combined and used to estimate the model parameters. Sample to sample comparisons may then be made at some prescribed level (usually $w = 1$) and changes in this "standard" catch with time or size can be used directly as estimates of mortality. Under the model assumptions, methods are described for obtaining maximum likelihood estimates of abundance and mortality with standard errors during the early life history which may then be used to examine the magnitude and pattern of variability in indexes of recruitment strength.

No attempt is made to justify the negative binomial model on a conceptual basis. Bliss (1971) suggests that it is as widely applicable for discrete counts as the normal for continuous data. Others (e.g., Taft, 1960; Roessler, 1973) describe the sample frequencies of a variety of organisms including fish eggs and adult fish. Anderson (1964) considered the model for the catch and effort relationship. An empirical evaluation of its use in the description of larval fish catches was central to this investigation.

EFFECTIVE SAMPLER SIZE

Environmental and behavioral factors act together to alter the chance of capture and retention of organisms even for standard gear and operational procedures in all fishery resource surveys. These factors interact to produce what is called the "effective sampler size." For example, avoidance behavior and extrusion through the mesh operate at opposite extremes of the size range to determine a size-specific

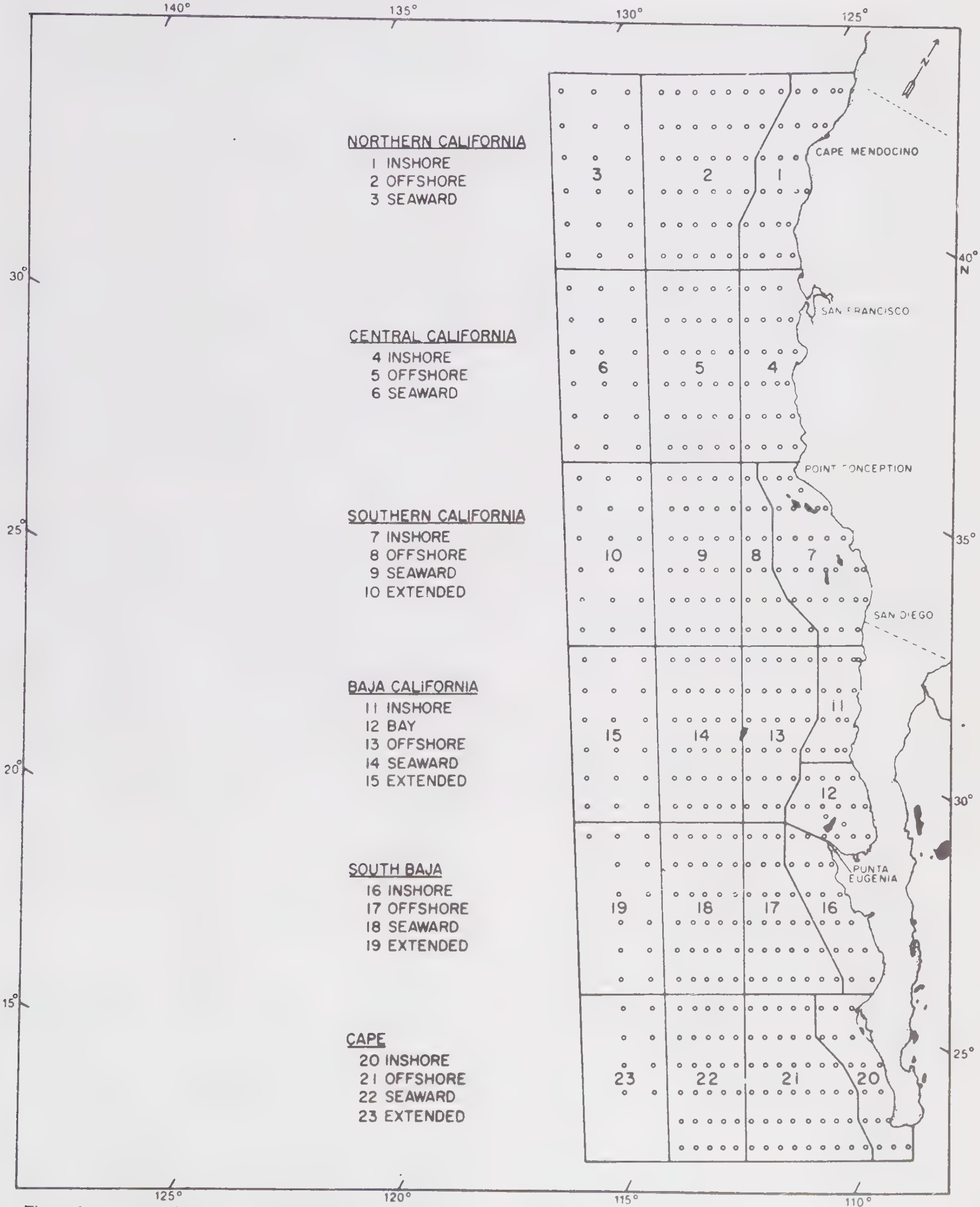

Figure 1. Areal regions used in the analysis of larval catches. o denotes station to be sampled.

catchability. In contrast, a fundamental requirement of all statistical sampling is that the sampler size be constant or at least measurable. Only when it is constant can sample to sample comparisons be made based on the empirical variability; otherwise, expected frequencies and thereby all sampling efforts become inextricably confounded with variations in real abundance of the organism in the environment. In the NBW model, both the mean and variance of each observation are determined by the "effective sample size" w_i, i.e., $E(x_i) = mw_i$ and $\sigma^2(x_i) = mw_i(1+mw_i/k)$ where w_i is determined from other variables measured coincident to the time of collection.[2] Zeros or empty samples are assigned a finite probability of occurrence and treated as real rather than "pseudo" observations. The expected catch under specified "standard" conditions (w=1) appropriate for estimates of abundance and mortality, is the parameter m without recourse to transformation. The parameter k is an estimate of contagion in the disposition of the sampled organisms.[3] Iterative procedures are required to obtain the maximum likelihood solutions for the parameters m and k and the asymptotic variances. The maximum likelihood equations are given by Bissell (1972). Algol coded solutions are available at the SWFC.

Maximum likelihood solutions for the parameters of any mortality relationship using the means (m) of several distributions and time or age may be obtained by generalizing the probability function

$$\Pr(x_{ij}) = f(m_i, k_i, w_{ij})$$

to include a relational expression of the individual means with an independent variable(s) e.g., $\tilde{m}_i = \theta_i \exp(-\theta_2 s_i)$ so that the probability of any x_{ij} is defined as

$$\Pr(x_{ij}) = f[\theta_i \exp(-\theta_2 s_i), k_i, w_{ij}]$$

Iterative procedures are then employed to obtain the maximum likelihood solution for the parameters and variance-covariance matrix (Zweifel, unpubl. ms.a). Variance estimates for the means are based upon the propagation of error approximation (Deming, 1966, pp. 130). For the simple exponential model above,

$$\mathrm{Var}(\tilde{m}_i) = \exp(-2\hat{\theta}_2 s_i) * [\hat{\mathrm{Var}}\,\theta_1 + (\hat{\theta}_1 s_i)^2 \hat{\mathrm{Var}}\,\theta_2 - 2\hat{\theta}_1 s_i$$
$$\hat{\mathrm{Cov}}(\theta_1 \theta_2)]$$

METHODS

Numbers of larvae and associated tow data were grouped by station within region and season. The set of samples consisted of oblique plankton tows with a 1m diameter net from below the recorded depth of the anchovy larvae to the surface. A detailed description of the sampling method used is given in Kramer et al., (1972). A statistical summary of the samples is given in Smith (1972). All preserved anchovy larvae in the collection were recorded in length classes given in Table 1, Columns 1–3.

An "effective sampler size" was calculated for each factor thought to seriously bias the estimates of abundance. The most obvious biases are extrusion through the mesh, avoidance of the net mouth, and variation in the amount of water strained per meter of depth. Another less obvious but potentially equally important factor is the influence of water temperature on embryonic growth rate. Size specific and differential growth rates could seriously bias the estimate of duration of the size categories, and thus estimates of absolute or relative abundance and mortality. Methot and Kramer (1979) suggest that possible temperature effects may be less than anticipated because of compensatory effects of food availability and larval behavior.

Avoidance corrections are based upon long term (20 years) catches by size and time of day. Adjustment for the effects of temperature on duration within a size interval are obtained from a temperature dependent growth model developed in the La Jolla Laboratory of NMFS (Zweifel and Lasker, 1976). Escapement through the meshes of the net as a function of larval length is estimated from empirical field data (Lenarz, 1972). A calibrated flowmeter in the net was used to measure the volume filtered per tow. All four bias adjustments were combined for each larval size category in each sample to yield a single "weighting factor." This factor (w) was the product of the four separate bias adjustments and was a measure of the "effective sampler size" for a particular collection and size range of larvae. The weighting factor (w) is unity when no extrusion takes place, avoidance is minimal[4], 3.50 m^3 of water were strained per meter of depth, and the temperature at 10 m depth was 16.2° C.

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[2] In an alternative formulation (Bissell 1972b), $\sigma^2(x_i) = mw_i(1+\frac{m}{k})$. We have not, as yet examined this model in our work.

[3] Mathematically, there is no requirement that areas of high or low abundance be contiguous. Larval disposition nearly always exhibits recognizable areal and/or temporal continuity; thus, we interpret the parameter k as a measure of real contagion. Recently, however, Taylor et al. (1979) have stated that the behaviour of k (actually 1/k) is complex in theory and an inconsistent measure of aggregation in practice, whether the negative binomial fits the data or not.

[4] On the basis of larval catches from the period 1951–1969, minimum avoidance of all sizes occurs between 2200 and 2300 h. We used catch at 2300 hours as the standard for all sizes. At least for large larvae the possibility of absolute avoidance cannot be dismissed; thus abundance of these size classes may be underestimated and mortality rates calculated for the entire size range may be too large.

Table 1. Estimates of live[a] size at age of anchovies for the classes of preserved larvae[b] regularly taken during CalCOFI surveys and the estimated "effective sampler size" w for a standard volume of water strained during a tow at time of maximum catch (2300 h).

Group	Preserved size	Recorded size	Live size		Average size	Age from hatch	Days in interval	Weight factor[c] "w"		
			Begin	End				13°	16.2°	19°
0	0.0– 0.5	0.00	0.02	2.52	0.72	−1.31	2.47	0.60	0.37	0.27
1	2.0– 3.0	2.50	2.52	3.94	3.23	0.67	1.95	0.63	0.39	0.28
2	3.5– 4.0	3.75	3.94	5.04	4.49	5.14	4.69	2.11	1.30	0.93
3	4.5– 5.0	4.75	5.04	6.10	5.57	8.01	2.67	1.59	0.98	0.71
4	5.5– 6.0	5.75	6.10	7.15	6.62	10.53	2.40	1.73	1.07	0.77
5	6.5– 7.0	6.75	7.15	8.17	7.66	12.83	2.21	1.79	1.10	0.79
6	7.5– 8.0	7.75	8.17	9.18	8.68	14.96	2.07	1.68	1.04	0.74
7	8.5– 9.0	8.75	9.18	10.19	9.68	16.98	1.97	1.60	0.99	0.71
8	9.5–10.0	9.75	10.19	11.19	10.69	18.91	1.90	1.54	0.95	0.68
9	10.5–11.0	10.75	11.19	12.18	11.69	20.78	1.85	1.49	0.92	0.66
10	11.5–12.0	11.75	12.18	13.18	12.68	22.61	1.81	1.46	0.90	0.65
11	12.5–13.0	12.75	13.18	14.18	13.68	24.40	1.78	1.44	0.89	0.64
12	13.5–14.0	13.75	14.18	15.17	14.68	26.17	1.76	1.43	0.88	0.63
13	14.5–15.0	14.75	15.17	16.17	15.67	27.93	1.76	1.42	0.88	0.63
14	15.5–16.0	15.75	16.17	17.15	16.66	29.66	1.71	1.38	0.86	0.61
15	16.5–18.0	17.25	17.15	19.16	18.15	32.29	3.55	2.87	1.77	1.27
16	18.5–20.0	19.25	19.16	21.18	20.17	35.87	3.62	2.93	1.81	1.30
17	20.5–22.0	21.25	21.18	23.21	22.19	39.55	3.75	3.03	1.87	1.34
18	22.5–24.0	23.25	23.21	25.24	24.22	43.38	3.93	3.18	1.96	1.41

[a] Shrinkage corrections are based on the work of Theilacker (1980).

[b] Zweifel and Lasker (1976) assign a development equivalent length to eggs (Group 0) in order to utilize the same equation for development and growth.

[c] At 2300 h and 3.5 m^3 water strained per meter of depth.

Table 2. Number of 3.75 size class larvae taken in January, February and March of 1969 in southern California inshore Region 7 by station with hour, temperature at 10 m depth and standard haul factor = 10/volume strained/depth. Stations are identified in Kramer et al. (1972).

	January				February			
Station	Hour	Temp	SHF	Larvae	Hour	Temp	SHF	Larvae
80.51	17.98	13.06	2.99	9	05.03	13.22	3.41	69
.52	19.88	13.02	3.15	3	03.20	13.29	3.48	28
.55	22.23	13.22	3.42	21	00.10	12 85	3.82	1
.60	12.82	12.82	3.29	0	20.18	12.84	4.36	0
82.47	14.70	14.07	3.15	84				
83.40	08.95	14.31	.73	291	06 67	13.51	1.89	51
.43	11.55	14.43	3.22	343	10.12	12.90	3.67	18
.51	04.35	13.46	2.95	45	19.35	12.58	3.97	1
.55	01.35	13.29	3.26	0	22.43	13.17	3.29	4
87.33	21.93	14.20	2.35	115	17.25	14.20	2.60	103
.35	00.38	14.76	3.44	149	20.12	13.87	2.99	244
.40	03.12	14.03	3.25	550	21.78	13.89	3.44	88
.45	05.78	14.26	3.02	311	00.68	14.07	3.34	114
.50	08.22	13.44	2.95	14	03.18	12.80	2.93	10
.55	10.47	14.31	3.29	7	05.87	13.31	3.41	191
90.28	12.28	14.49	3.36	144	00.78	14.33	3.34	390
.32	09.05	14.79	3.29	223	22.18	14.63	3.17	1 012
.37	06.28	14.96	3.37	370	18.97	14.86	3.24	275
.39					15.68	14.80	3.48	243
.45	01.07	13.44	3.35	35	12.10	13 93	3.23	195
.53	20.77	14.68	3.30	632	09.37	13.80	3.20	84
93.27	09.93	14.03	2.89	21	05.32	14.36	2.72	820
.28	11.98	14.12	3.34	2	06.78	14.38	3.05	287
.30	14.07	14.05	3.25	4	09.37	14.45	3.45	1 343
.35	17.12	15.52	3.18	2	15.40	14.45	3.02	843
.40	19.93	14.31	3.20	118	20.28	14.78	3.19	115
.45	22.88	15.42	3.12	2	23.10	13.96	3.11	254
.50	01.72	15.56	3.39	0	01.68	14.65	3.14	385
94.30	07.37	14.31	2.97	46	17.03	13.91	3.29	354
97.29	12.57	14.88	2.04	44	09.10	14.22	2 60	120
.30	13.85	15.02	2.82	7	08.52	14.18	2.53	77
.32	17.28	15.08	2.81	18	07.53	14.35	3.14	79
.35	20.52	15.04	2.59	0	04.20	14.35	3.13	34
.40	01.10	15.48	3.00	0	01.40	14.20	3.18	117
		March						
90.45	09.10	13.72	3.31	282				

Table 3. Abundance classes of 3.75 mm larvae taken in the first quarter of 1969 in the southern California inshore Region 7 with average effective sampler size," age at 16.2° C, and corrections for bias due to temperature, volume of water strained, avoidance and extrusion.

Lower–Mark–Upper	No. of stations	Weight[a]	Age[b]	Temp[c]	Vol.[d]	Avoid[e]	Escape[f]
0	6	1.28	7.02	3.20	.88	.73	.63
1	2	1.04	8.75	3.99	.73	.56	.63
2	3	.85	6.10	2.78	.89	.54	.63
3	1	1.10	8.30	3.78	.91	.51	.63
4	2	1.53	7.55	3.44	.87	.80	.63
7	2	.96	6.40	2.92	.94	.56	.63
9	1	1.06	8.24	3.76	.95	.47	.63
10	1	1.79	8.62	3.93	.97	.74	.63
14	1	.75	7.73	3.53	.97	.35	.63
16– 21–32	5	1.21	7.49	3.42	.89	.64	.63
33– 43–64	6	1.63	7.12	3.24	1.10	.74	.63
65– 99–128	13	1.21	6.96	3.17	.94	.65	.63
129–205–256	8	.93	6.84	3.12	.87	.54	.63
257–329–512	10	1.28	6.68	3.04	1.19	.58	.63
513–771–1024	5	1.55	6.62	3.02	.93	.88	.63
1025–343–2048	1	.80	6.59	3.01	.83	.51	.63

[a] Average product of individual weighting components.

[b] Calculated from equations obtained from laboratory growth experiments. Temperature Specific Equations for growth and development of anchovy, *Engraulis mordax*, during embryonic and larval stages.

[c] Calculated as estimated time in size interval/standard time = 2 days.

[d] Calculated as estimated volume of water strained/standard volume = 3.5 m^3 per meter depth.

[e] Calculated as long term catch by hour/standard or maximum catch at 2300 h.

[f] Determined from mesh retention study of Lenarz (1972).

EXAMPLE

We use the numbers of 3.75 mm larvae collected during January, February and March of 1969 from the southern California inshore Region 7 as shown in Figure 1 to illustrate the steps required to calculate larval abundance from numbers of larvae per sample and associated data. Station by station larval counts together with the mid-time of haul, temperature at 10 m depth and standard haul factor (10/volume strained/depth) are shown in Table 2. In Table 3, the same data are grouped by classes of abundance. Grouping by abundance class is convenient, but is not a requirement of the NBW analysis. It is used here to average out the effects of the weighting factors. Preliminary investigation suggests that the effect on parameter estimates is minimal but further investigation is needed. O'Carrol (1962) assigned the interval frequency at the mid-point rather than the average. For each abundance class, the average bias correction for the four separate components, the average combined weight calculated as the average product of the individual components, and the estimated age at 16.2° C are shown.

Calculations analogous to those in Table 3 are required for each size class included in estimates of larval mortality. These bias corrections can significantly alter estimates of abundance at any size as well as the pattern of mortality from size class to size class. In Table 4, we show the uncorrected average number of larvae per sample $\bar{x}$ and the parameter estimates $\hat{m}$ and $\hat{k}$ with standard errors for all larval sizes (Jan–Mar, Region 7). The ratios $\hat{x}/\hat{m}$ indicate the effect of the weighting technique on estimated larval abundances; for these collections, a maximum (about two-fold) alteration occurs in the class of smallest larvae.

Estimated abundances $\tilde{m}_i$ assuming a constant instantaneous rate of size (average live length) — related mortality (θ_2) over the entire size range, i.e.

$$\tilde{m}_i = \theta_1 \exp(-\theta_2 s_i)$$

are also shown in Table 4 for the 16 smallest classes of sized larvae (January–March, Region 7, 1969). These estimates were obtained from the complete maximum likelihood solution where

$$\hat{\theta}_1 = 1780.05,\ \hat{\theta}_2 = 0.4717, \sqrt{\mathrm{Var}\,\theta_1} = 275.10 \text{ and}$$

$$\sqrt{\widehat{\mathrm{Var}}\,\theta_2} = 0.0159$$

The 2.50 mm size class has many more larvae than would be expected assuming continuity in the mortality relationship (Fig. 2). This class (<4 mm live size) precedes the "critical period" of first feeding larvae. (4–5 mm live size) whose biological importance has

Table 4. Estimates of the parameters of the negative binomial weighted model in the analysis of anchovy larvae taken during the first quarter of 1969 in Region 7.

		Actual counts		NBW estimates				Constant instantaneous mortality $\tilde{m}_S = \hat{\theta}_1 e^{-\hat{\theta}_2 S}$		
Class	Average live size (mm)	$\bar{x}$	s	$\hat{m}$	s_m	$\hat{k}$	s_k	$\tilde{m}$	k	Var in $\tilde{m}$
250	3.23	338.05	620.50	801.83	176.189	0.310	0.0461	387.51	0.268	0.0118
375	4.49	176.77	253.51	159.06	30.631	0.403	0.0613	213.86	0.393	0.0086
475	5.57	91.58	109.07	111.47	20.894	0.428	0.0690	128.51	0.424	0.0065
575	6.62	52.77	61.88	56.94	9.906	0.500	0.0829	78.22	0.480	0.0050
675	7.65	31.80	38.56	40.67	7.050	0.506	0.0869	48.06	0.500	0.0040
775	8.67	17.25	21.33	24.69	4.100	0.567	0.1040	29.72	0.556	0.0036
875	9.68	11.29	15.50	16.68	3.048	0.471	0.0929	18.47	0.468	0.0037
975	10.68	8.29	13.20	12.54	2.690	0.345	0.0739	11.51	0.344	0.0044
1075	11.68	5.43	9.72	9.74	2.016	0.380	0.0859	7.18	0.359	0.0055
1175	12.68	2.46	5.55	4.74	1.122	0.312	0.0878	4.49	0.311	0.0071
1275	13.67	1.73	5.04	3.77	1.289	0.145	0.0450	2.80	0.141	0.0092
1375	14.67	1.08	3.66	2.11	0.840	0.111	0.0407	1.75	0.110	0.0118
1475	16.17	0.65	2.29	1.16	0.460	0.112	0.0488	0.86	0.106	0.0167
1575	16.65	0.32	1.23	0.52	0.281	0.064	0.0381	0.68	0.063	0.0185
1725	18.15	0.25	0.84	0.24	0.100	0.137	0.0847	0.34	0.129	0.0247
1925	20.16	0.17	0.85	0.13	0.088	0.046	0.0340	0.13	0.045	0.0348

been the subject of considerable study and speculation. For the biological point of view size classes, 2.50 and 3.75 mm are subject to increased variability due to the unpredictable nature of the time of first feeding and the subsequent rapid increase in growth.

Several authors, e.g. Lasker (1975, 1978) and Hunter (1976) have documented the importance of food density as well as the capacity for high survival with minimum growth. Thus, departure from the "average" environmental condition may give rise to greater or lesser numbers of larvae in either the "critical period" or those adjoining. Failure to find food will increase the numbers remaining in the small (2.50 mm) size class and decrease the observed number of the 3.75 mm class. Above average feeding conditions promoting growth will tend to decrease the observed number in the non-feeding (2.50 mm) category and increase numbers in the 3.75 and subsequent size classes. Figure 2 (inset) shows the average or standard (16.2° C) growth relationship for newly hatched to 6 mm larvae together with similar curves for 13° and 19° C. To the extent that variations in food availability can be equated to changes in ambient temperature and thus to growth, the potential for increased variability in observed counts exists. In the next section, we show that even the large discrepancies in 2.50 mm class larvae may be more apparent than real.

CONFIDENCE INTERVALS

Establishment of useful limits or intervals requires a stable population and a representative sample from that population, neither of which can be assured in natural environments. In fact, it has been recognized (Taylor 1971, pp. 363; Taylor et al., 1979, pp. 290) that most sample frequency distributions are largely empirical in nature. For example, the negative binomial frequencies can arise from a variety of conceptual formulations or empirically by random sampling over a gradient (Taylor, 1971, pp. 362). Variations in absolute or "effective" sampler size may give rise to sample frequencies which reflect changes in catchability as well as areal-temporal disposition; then samples become an amalgam of observations and not even nonparametric methods of analysis are appropriate. As an alternative to confidence limits, Kempthorne (1967) and more recently Easterling (1976) propose the use of consonance regions or intervals which depend only upon the model formulation for the observed sample. This approach determines limits on the parameters of the frequency distribution such that the goodness of fit is contained within specified probability limits. While this seems the more realistic approach, it has so far been largely ignored by statisticians and biologists alike. We have not, as yet, explored the applicability of consonance regions to the Negative Bionomial Weighted (NBW) analysis, although an examination of these kinds of alternatives seems essential to any major advance in the application of realistic statistical procedures to natural or uncontrollable populations.

We have used the NBW model analysis to separate the effects of catch-ability and disposition. The recommendations for confidence intervals are based upon simulations from completely specified binomial, Pois-

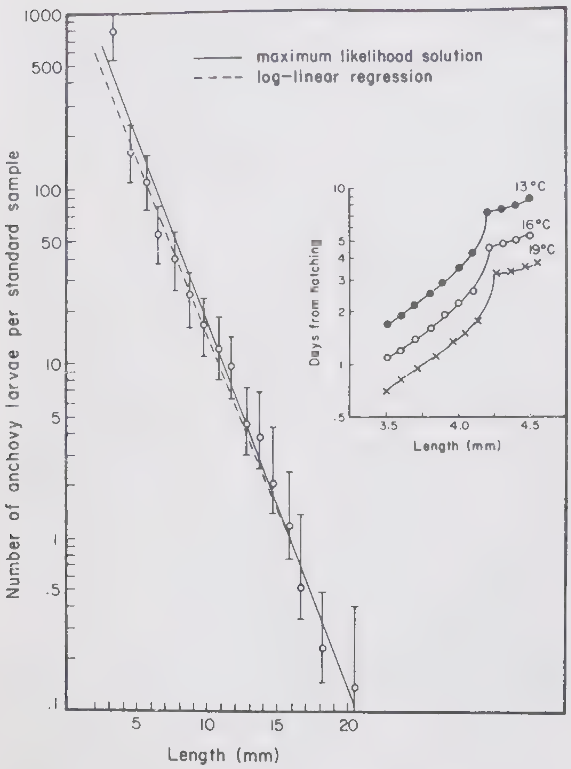

Figure 2. Estimates of the mean per standard sample ($\hat{m}$ of the NBW analysis) for 16 size classes of anchovy larvae with confidence intervals. Coefficients of the mortality relationship were estimated from both the NBW analysis (1780.05, 0.4717) and the regular log-linear regression (1855.10, 0.4740). Inset describes growth at three temperatures at the onset of feeding (4.28 mm).

son and negative binomial distributions (Zweifel, Unpubl. ms. b) and from simulations from known mortality relationships, e.g., where $\tilde{m}_i = \theta_1 \exp(-\theta_2 S)$. The former suggest that for the three models the distribution of the sample mean $\bar{x}$ is more closely approximated by the log-normal than the normal distribution, i.e., that the upper (UCL) and lower (LCL) confidence limits determined as

$$\mathrm{LCL} = \bar{x}\exp(-Z_p\sqrt{(\mathrm{Var}\ \ln \bar{x})})$$

and

$$\mathrm{UCL} = \bar{x}\exp(Z_p\sqrt{(\mathrm{Var}\ \ln \bar{x})})$$

where

$$\widehat{\mathrm{Var}}\ \ln \bar{x} = \ln(1 + \mathrm{Var}\ \bar{x}/\bar{x}^2)$$

and Z_p is the standard normal deviate such that $P_r(Z > Z_p) = p/2$, more nearly account for the asymmetries in the distribution of the sample mean for small sample sizes. As the sample size increases, the two become indistinguishable. Simulations of the mortality relationship indicated that the instantaneous mortality coefficient (θ_2) obtained from the maximum likelihood solutions were essentially normally distributed while the estimates θ_1 and $\tilde{m}$ were skewed and more closely approximated by a log-normal distribution. Detailed results will be presented in a separate paper.

In Table 5 we use equations (7) and (8) and the maximum likelihood estimates for the 16 smallest classes of sized larvae (Jan–Mar, Region 7, 1969) to calculate the 95% confidence limits for the estimates $\tilde{m} = \theta_1 \exp(-\theta_2 S)$, i.e. where $\bar{x} = \tilde{m}$ and Var $\bar{x}$ is estimated from equation (4). For comparison, we calculate the same limits using the simple regression of ln $\hat{m}$ on average size. These and other results suggest that the simpler procedure may provide estimates equally as useful as those derived from the complete maximum likelihood solution. Confidence limits calculated for an individual observation using the regression equation shows that the number of 2.50 mm class larvae is just slightly greater than the upper 95% limit.

ESTIMATES OF ABUNDANCE AND MORTALITY

ABUNDANCE

In a period of development and rapid growth of fish eggs and larvae, vulnerability to capture by the plankton net changes continuously and rapidly. When the areal-temporal distribution of the spawning population is extensive, changes in catchability due to behavioral and environmental factors may greatly alter both the bias and variability in the catches. To estimate the standing stocks apart from changes in catchability, we used the NBW model to estimate the abundance of each size of larvae together with standard errors for each region and season for the years 1951–75. The parameter estimates $\hat{m}$ for these analyses thus represent the catch which would have been expected for the standard or ideal sampler.

MORTALITY

For the steady state model[5] the variability inherent in estimates of mortality due to the spatial heterogeneity of the spawning habit of schooling pelagic fish (Smith, 1973) and subsequent dispersion from the centers of spawning has not as yet been separated from

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[5] On a population basis, the overall steady-state may not occur; spawning rate may not be continuous (Hunter and Goldberg, 1980), and the mortality rate may not be constant. Lenarz (1973) reported "catch curves" for some larvae of the California Current area and specified conditions for interpreting mortality rates. Under some conditions (Ahlstrom, 1954) it may be possible to trace "cohorts" of larvae as would be indicated by the analysis of the fate of a single short-term spawning.

Table 5. The 95% confidence limits of sample estimates by size-class using propagation of error and logarithmic slope approximations.

Size class	Size live (mm)	Propagation of error			$\ln \hat{m} = a + b * \text{Size}$				
					Mean			Predicted	
		LCL	m	UCL	LCL	m	UCL	LCL	UCL
2.50	3.23	311.84	387.51	481.54	309.60	397.89	511.34	210.12	753.43
3.75	4.49	177.66	213.86	251.44	176.73	219.13	271.72	117.26	409.51
4.75	5.57	109.37	128.51	151.00	109.23	131.42	158.13	71.01	243.22
5.75	6.62	67.90	78.22	90.10	68.36	79.94	93.49	43.54	146.78
6.75	7.66	42.38	48.06	54.58	42.92	48.86	55.63	26.78	89.15
7.75	8.68	26.37	29.73	33.52	27.12	30.15	33.51	16.60	54.74
8.75	9.68	16.35	18.47	20.86	17.23	18.78	20.47	10.37	33.99
9.75	10.69	10.08	11.51	13.14	10.81	11.64	12.53	6.44	21.04
10.75	11.69	6.20	7.19	8.34	6.74	7.25	7.80	4.01	13.10
11.75	12.68	3.79	4.49	5.31	4.18	4.54	4.93	2.51	8.21
12.75	13.68	2.32	2.81	3.40	2.55	2.83	3.13	1.56	5.13
13.75	14.68	1.41	1.75	2.18	1.55	1.76	1.99	.97	3.21
14.75	16.17	.67	.86	1.12	.74	.87	1.02	.47	1.60
15.75	16.66	.52	.69	.90	.58	.69	.82	.37	1.27
17.25	18.15	.25	.34	.46	.27	.34	.42	.18	.64
19.25	20.17	.09	.13	.19	.10	.13	.17	.07	.25

variations in catchability. As noted above, this may be accomplished by incorporating the mortality function into the NBW analysis. In the regional-seasonal series reported here, the simple exponential model $\tilde{m} = \theta_1 \exp(-\theta_2 S)$ was adequate for the size range 3–20 mm[6]. Even so, in some cases, variations in sampling intensity prevented a maximum likelihood solution for mortality. To provide a continuous series, the mortality estimates are based upon the relationship of the log-transformed NBW estimates $\hat{m}$ and the estimated mid-live size at 16.2° C. As indicated in the section on confidence intervals, it does not appear that either bias or variability differ greatly for the alternative solutions.

The analyses included one fit to the first six size groups if present—one fit to the larger 12 size groups if present—and a fit to all size groups present. Cruises were conducted no more frequently than monthly and the maximum estimated age from spawning of 15 mm larvae is approximately 30 days at 16.2° C. Consequently, under a steady state model, each size group up to 15 mm may be used to estimate total egg production by the spawning population.

RESULTS

We examined only the simplest hypotheses concerning the relationship of larval abundance and mortality to recruitment strength. On average, estimates of mean abundance and mortality coincided with estimates of the strength of a year-class obtained from fishery data as reported by Smith et al. (this volume).The median mortality coefficient calculated from embryonic and early larval sizes for years above and below average strength were 0.24 and 0.32, respectively. The average abundance of 15 mm larvae interpolated from the analysis of larger larvae indicated differences between these same years.

Nevertheless, except for a few extreme cases, we were unable to quantitatively detect changes in recruitment potential from the average regional-seasonal estimates of embryonic or post-embryonic mortality or the abundance of 15 mm larvae. The failure may be an inherent problem in sampling the late larvae; or the determination of recruitment level may be established in subsequent months of development and survival of larvae, post-larvae, and juveniles. It is also possible that increased recruitment may come from high survival in certain (e.g., nearshore) regions rather than from general increases over the total geographic area.

Relatively small areal-temporal strata[7] (20 000 square miles over 3 months) often yielded estimates of abundance and mortality which were biologically and

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[6] Analyses over extensive ranges of size or age or from life stage to life stage indicate, however, that time or size dependent mortality rates such as those defined by the equation

$$dN_t/dt = (\alpha + \beta\rho^t)N_t \text{ or } N_t = N_0 e^{k(R^t-1)^{-ct}}$$

are required to estimate the decline in the observed counts.

[7] Some of the arbitrarily selected strata used in this study contained more gradients or large-scale heterogeneity than could adequately be described by the NBW model, at least with the weighting factors used herein. These strata cannot be determined a priori nor changed retrospectively; their discovery was in fact an important objective of this study. It should be noted, however, that smaller strata exhibiting statistical coherence are more subject to the effects of drift into and away from the strata of birth altering the estimates of mortality in contiguous areas or seasons.

Table 6. Seasonal estimates of anchovy larval mortality (number per mm) in Region 7 for the years 1951–75 and estimates of relative year-class strength[a].

	Jan–Mar	Apr–Jun	Jul–Sep	Oct–Dec	Year-class strength
1951	.05	.38	.29	.33	−2.76
1952	.25	.27	.22	.33	− .66
1953	.35	.25	.47	.48	1.98
1954	.47	.42	.29	.45	3.30
1955	.44	.40	.23	.14	−1.92
1956	.36	.43	.26	.28	−2.82
1957	.44	.45	.26	.34	−2.94
1958	.51	.40	.32	.45	− .42
1959	.48	.41	.29	.30	4.08
1960	.47	.37	.24	.09	.42
1961	.59	.47	.30	.09	− .30
1962	.56	.43	.33	.25	.96
1963	.58	.28	.31	.32	3.42
1964	.44	.41	.31	.30	1.62
1965	.67	.49	.50	—	−2.34
1966	.50	.55	.38	.43	−3.12
1967	—	.34	.31	—	.60
1968	.48	.53	—	—	.60
1969	.47	.56	.44	.47	.72
1970	—	—	—	—	3.18
1971	—	—	—	—	1.14
1972	.50	.53	.42	.42	1.44
1973	—	—	—	—	.48
1974	—	—	—	—	3.66
1975	.49	.72	.49	.50	−4.68

[a] Based on the average normalized contribution of 1,2,3 and 4 year old fish to the commercial catch.

statistically reasonable. Mortality estimates from one stratum (Region 7) within the population center were remarkably stable over large changes in estimated year-class strength (Table 6). These results suggest (a) that pooling of mortality information over years and/or seasons may provide more precise estimates of abundance and; (b) that concentration of sampling within the population center may preclude the detection of important changes in recruitment potential.

SAMPLE SIZE

English (1964) noted that concentration of sampling effort in time or space is hazardous unless the spawning behavior of the population is well understood. The non-random distribution of eggs and larvae insures that the inherent variability changes with levels of abundance and makes extrapolation of sampling requirements difficult.

We consider the case where estimates of the negative binomial parameters m_1 and k_1 are available from sampling the time and area of peak spawning. Under the model the coefficient of variation ($S_{\bar{x}}/\bar{x}$) of the sample mean C_1 is $\sqrt{(1/n_1m_1+1/n_1k_1)}$ where n_1 is the number of samples or collections. For an alternative plan, the corresponding expression is

$$C_2 = \sqrt{(1/n_2m_2+1/n_2k_2)}$$

For fixed intervals of sampling (both in time and space) expansion of the sampling grid outside the area of peak spawning reduces both the mean m_2 and coefficient of contagion k_2, approximately by the ratio $\sqrt{(n_1/n_2)}$. Adjusting the algebra, we obtain

$$C_2/C_1 = \sqrt[4]{(n_1/n_2)}$$

Thus a doubling of the sample size obtained by increasing the sampling area, i.e., $n_2=2n_1$ may be expected to decrease the relative standard error by only 16% to $\sqrt[4]{(1/2)} = 0.84$. Similarly a ten-fold increase in area gives $C_2/C_1 = 0.56$ i.e., less than 50% reduction. On the other hand, a four-fold decrease ($n_2=n_1/4$) increases the ratio by only 40%. Changes in sampling intensity, i.e. where $m_2=m_1$ and $k_2=k_1$ alter the ratio C_2/C_1 as $\sqrt{(n_1/n_2)}$. Within the area of peak spawning, for example, a four-fold increase in sample size will be required to reduce the relative coefficient of variation by half. Thus the a-fold change in sampling intensity required for a b-fold change in range in order to attain a P percent change in the relative coefficient of variation is determined by the relationship

$$(1-P/100) = a^{-1/2}b^{-1/4}$$

The solutions for a given P = 0(25)75 and b = 0.25, 0.50, 1(1)4 are shown in Table 7. Taylor, et al. (1979) examined the density of k and showed that m and k are not functionally independent. That interaction has not been considering here. The form of the relationship if known, could lead to more precise estimates of the sampling requirements.

The relationship for fixed k, $m_2 = am_1$ and $n_2 = bn_1$ is

$$C_2/C_1 = \sqrt{\left[\frac{1}{b}\left(1 - \frac{a-1}{an_1m_1C_1 2}\right)\right]}$$

While approximate, these relationships indicate the intensity of sampling effort required for specified precision in the estimates of abundance and mortality and thus for indexes of stock size and recruitment.

DISCUSSION

In this paper we describe a statistical model for the expected frequencies of the catches of eggs and larvae taken in large scale oceanic surveys which permits sample to sample comparisons and which is robust against changes in both the form of the underlying distribution and the mechanisms which determine them. The negative binomial distribution on which the analyses are based is suited without change to the Poisson at one extreme and the Poisson log-normal at the other extreme of "patchy" disposition. Patterns of mortality and dispersal and subsequent reaggregation common in the life cycle of pelagic schooling fish can be analyzed without change of the underlying distributional model. The effects of uncontrollable variations in the "effective sampler size" and size and density dependent levels of aggregation are incorporated as a fundamental part of the estimation procedure.

Table 7. Estimates of the a-fold change in sampling intensity required for a b-fold change in sampling range in order to attain a P percent change in the relative coefficient of variation $S_{\bar{x}}/\bar{x}$.

	b					
P	.25	.50	1	2	3	4
0	2.0	1.4	1.0	.70	.58	.50
25	3.6	2.5	1.8	1.2	1.0	.89
50	8.0	5.6	4.0	2.8	2.3	2.0
75	32.0	22.6	16.0	11.3	9.2	8.0

Using the NBW analysis, bias corrections for size, water filtered, time of day, and growth can be augmented by other as yet unquantified correction factors without fundamental change in the analysis. Existing correction factors can be separately or jointly evaluated for impact on sample variance and requirements for careful conduct or planning of tows can be relaxed or tightened as deemed appropriate. Alternative sampling designs (including fractional sorting) can be examined from existing data with known impact on both the estimates of standard error of density and the geographic area of occurrence. Empirical approaches can be attempted; multivariate and numerical classification techniques using the estimates of abundance, aggregation, coverage and mortality may uncover hitherto unrecognized relationships which are indicative of changes in absolute or relative recruitment.

The lack of simple relationships among abundance, survival and recruitment strength is not surprising: e.g., critical geographic or temporal scales may exist for determining mortality rates at different stages of the life cycle and incorporating them into a useful estimate of the level of recruitment. The existence of such scales may be explored experimentally (e.g., by intensive surveys of small subareas of the larval distribution) to detect local differences in larval survival and to forecast the impact of those differences on the recruitment of the young to the fishable stock (see e.g., Lasker, this volume) or by retrospective data analysis. The success or failure of either will be determined by the variability inherent in the sampling process and the sampling effort. In uncontrolled environments, variability is due to (a) changes in the effectiveness of the sampler. (b) the sampling design and intensity, (c) the method of analysis, and (d) the areal-temporal disposition of the population. In this paper we have addressed the first three of these issues from a statistical point of view. The last issue is variable but not statistical, i.e., it is basically unpredictable. No amount of statistical information can determine the practical risks involved in limiting the sampling range. Restriction of sampling to population centers without corresponding changes in sampling intensity may decrease rather than increase precision in the estimators. We have attempted to provide estimates of the cost (in terms of sample size) of limiting the sample range without significantly impairing the reliability of the results.

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